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MATHEMATICAL BIOLOGY

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BY

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WITH A PREFACE BY
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CONTENTS

PREFACE

A NUMBER of original works on the application of
mathematics to biology have been published during
the past few years, but there is still no work of a
synthetic and didactic type, bringing together all the
research on this subject. M. Kostitzin's book fills
this gap.

M. Kostitzin is a very distinguished mathematician.
He is thoroughly familiar with all the resources of
analysis and its most recent applications. He has
shown his ability and skill by solving problems that
had defeated the efforts of his predecessors.

But to deal with questions of an entirely novel kind,
such as those with which M. Kostitzin is concerned, it
is not enough to be a good geometrician; other gifts
and other abilities—found in the highest degree in this
book—are necessary, as well as extensive knowledge
beyond the regions of pure mathematics.

M. Kostitzin himself clearly expresses this idea in
the first chapter of this work, in which there will be
found many general considerations on mathematical
reasoning, on fundamental hypotheses in general
science, on statistical methods and on the many sources
of error in passing from experiment to analysis and in
trying to arrive at general laws. This philosophical
viewpoint at once gives the reader a favourable im-
pression of the spirit in which the work is conceived.

The book begins with general mathematical ideas
on the frequency curves, the correlation of phenomena

and the differential equations that are encountered in biology. It next goes on to the general laws governing the circulation of organic matter, of carbon, oxygen, and nitrogen, which give a synthetic idea to life and its environment.

One chapter is devoted to the Logistic Law, first stated by Verhulst and so often applied and verified by Pearl and other statisticians.

The consequences of these problems of multiplication, taking the most varied factors into account, form a new chapter. In particular a study of poisoning due to the products of metabolism will be found; the experimental work of Régnier and Lambin is familiar; I had taken up the question from a mathematical point of view, obtaining an integro-differential equation which I had simplified and reduced to a differential equation.

But it is to M. Kostitzin that the integration of this equation is due, an integration accomplished in a very ingenious manner, as will be seen in this book. This result has both a mathematical and a biological interest, and offers a fine example of the analytical audacity of M. Kostitzin.

I have one comment to make on this point. In this particular problem it has been possible, by an artifice, to avoid integration of the integro-differential equation and to reduce it to a differential equation, but it is clear that integro-differential equations cannot always be avoided, and that they must play a part in biological problems.

I shall not go into details of a host of examples in which the author studies population, the fluctuations and the growth of a population composed of several species,

taking into account food obtained directly from the environment or by the species eating each other.

From this group of ideas we pass easily to the study of symbiosis and parasitism, and so to the growth of organisms and of tissues considered on the lines of a population. But the author carefully avoids pushing this comparison too far; he shows the essential difference which must exist between a case in which the components of a group are independent and one in which they are not. In an organism the functions of the different elements, and their ways of nourishing and reproducing themselves, must be taken into consideration.

In order to omit nothing that can be examined from a geometrical point of view, the author also deals with the form of living objects and the work ends with a general discussion of evolution and selection, in which mathematics plays a very important part.

In the treatment of all these questions the author shows perfect familiarity with the many researches carried out by naturalists, especially recently, and his work successfully combines mathematical and experimental studies. To give an idea of the superposition and of the necessary fusion of fact and theory, the author employs a very striking image, drawn from romantic literature.

It is unnecessary to add that the book will be of the greatest value to naturalists, and that it will give mathematicians a host of problems to investigate. From the point of view of the progress of mathematical biology, a new science that is developing so rapidly and so successfully, the publication of M. Kostitzin's book marks a very important date.

VITO VOLTERRA.

CHAPTER I

INTRODUCTION

1. THE PURPOSE OF THIS BOOK

THIS book is intended for biologists who are to some extent familiar with mathematical analysis, and for those mathematicians who, being naturalists, do not believe that the sole aim of mathematics is the enunciation of formulae. I have tried to discover the relations between my methods and their results, but in this region of learning, where so much is still to be done, the disparity between its methods and reality is often evident. From this there follows the appearance of duality which this book presents, as if it were composed of two different works whose pages had been intermingled. Literature includes a well-known example of this in the *Kater Murr* of the famous German writer, E. T. A. Hoffmann. In that book the matter of fact philosophy of a cat is contrasted with the shafts of wit, the dreams and the romance of Kreisler, the musician. Anyone who has read the *Kater Murr* realises that in spite of its rambling appearance, the book possesses a deep inner unity. There is romanticism and realism in my book, but there is unity as well. If I have not always succeeded in making it manifest, it is sometimes because the problem does not lend itself to this treatment and sometimes because the biological material was lacking.

This little book differs from other works published under similar titles, which are rather text books of

mathematics for biologists than a mathematical study of biological problems. I do not deny the value of such works for information, for quick reference, etc., but I do not believe that such a selection of certain sections in one science for the use of workers in another can be successful. Each science has its own language and its own logic, and it is only by keeping to its own principles that it can retain its full value in applications. It is impossible to say what portions of a science are necessary and what are superfluous in any given application. It would be interesting to review all the mathematical text books published during the last fifty years intended for physicists and naturalists, beginning with that of H. A. Lorentz (1882). One would see how certain sections, long neglected by physicists and yet very important from the mathematical point of view, suddenly appeared and took a prominent place in these works. A biologist who has need of chemistry ought thoroughly to study that science, and not a few sections specially selected and adapted. In the same way, to be able to apply mathematical methods it is necessary to study what constitutes the very essence of these methods—their ideas—and not a few applications of the calculus. It is of greater value to consult a logically ordered text book than a compilation including scraps of analysis and odds and ends of the calculus of probabilities, decked out with biological examples that have often been dragged in by the scruff of the neck.

In the following pages I have given a collection of biological problems capable of mathematical treatment. These are the problems of the multiplication of groups of organisms and of the organism itself considered as

a complex of cells or of organs, or as a thermal machine, or as a major unit composed of, but not reducible to, a number of minor units. From the mathematical point of view, all the problems considered present a certain unity. The fundamental ideas, the variables that are used, the co-efficients of the equations, are the result of long statistical elaboration, but the logical apparatus is purely analytical. The equations nearly all belong to the type of differential equations or integro-differential equations of the first order. That rich mine, opened independently by A. J. Lotka and V. Volterra is far from being exhausted. Numerical results are not always reached, but qualitative results are obtained, the only ones capable of verification, because the numerical biological material with which they deal is too uncertain or too heterogeneous for accurate corroboration.

I should like to thank Madame J. Kostitzin for her invaluable help. I thank sincerely M. E. Rabaud and M. P. Montel, who agreed to the inclusion of this work in the *Collection Armand Colin.* I am most grateful to M. M. Prenant, who has done me the kindness of reading the manuscript, and to M. G. Teissier, whose conversation has given me many interesting suggestions, and to M. Régnier, who sent me his experimental results. I am particularly grateful to M. Vito Volterra for the encouragement that he has never ceased to afford me.

2. Mathematics and Natural Science

The history and the logic of Science teach us that the application of mathematics to science is an inevitable

stage and a necessary condition of its development. Mathematics itself conceals under its array of logic an empirical foundation, sometimes so hidden by superstructures that mathematicians forget its very existence. It is this basis which comes into play every time one appeals to common sense, it is this that is discussed in the study of the logical and psychological foundations of infinitesimal analysis.

Everyone is agreed that figures have the right of entry into Natural Science, but when it becomes a matter of reasoning about these figures, or of dealing mathematically with them, there is encountered a resistance, a repugnance. Why is this? It must be admitted that this resistance does not always come from narrowmindedness or from conservatism. Reasoning in general does not frighten a naturalist, but mathematical reasoning startles him, because he is in the habit of verifying each step by experiment. In reasoning, experimental results are subjected to a series of logical operations. The accuracy of the ultimate result depends on that of the initial data, and also on the number and nature of the logical operations carried out between the premise and the conclusion. In ordinary reasoning, this number is not very great, and successive stages are always verifiable. In mathematical reasoning, the steps are taken too quickly, and a result is reached which may appear to be, and very often is, arbitrary or untrue. The reason for this is that in establishing a biological equation, the problem is simplified by sacrificing a number of factors or a number of details, and these sacrifices distort the results that emerge from the logical method. Inexact yet acceptable initial hypotheses are transformed into

gross errors by a few turns of the crank of the logical apparatus. Simplification gives rise to paradox. This is a fact that cannot be denied, and one that is common to all experimental sciences. In purely mathematical problems, the mathematician is certain of his premise and the number and nature of the operations is of interest only from the aesthetic point of view; but in dealing with applications of mathematics, the position is quite different. A long period of development has been necessary to secure unquestioning acceptance of the agreement between reasoning and experiment in mechanics, physics and astronomy. Perhaps in biology this development will be more rapid by virtue of an acquired impetus. In any case, long and continuous collaboration between mathematicians and biologists is necessary before reaching the same assurance as in the physical sciences.

3. THE STATISTICAL AND THE ANALYTICAL METHODS

Mathematics gained entry into Natural Science by the statistical door, but this stage passes to the stage of analysis as in all quantitative sciences. The function of the statistical method is to clear the ground, to establish a certain number of empirical laws, and so to facilitate the transition from statistics to analysis. The labour of doing this is considerable, and important, but when it is done the first duty passes to mathematical analysis, which, at this stage in the growth of a quantitative science, is alone able to trace out the causes of phenomena and to deduce from them all the logical consequences. At this stage even approximate hypotheses as to the true nature of the phenomena

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are often more useful than empirical laws, calculated *lege artis*, with all essential accessories. Thus Ptolemy, in his *Optics*, studies the problem of the refraction of light. He gives several results of experiments on the passage of light from air to water and from air to glass. His figures are quite sufficient to confirm Descartes' law. With these figures a modern investigator could construct a polynomial, reproducing them with exact precision, and could calculate their probable errors, but such a formula taken as a basis of research would be not only useless but misleading, and not even Descartes, had he been only a statistician, could ever have discovered the law of refraction. This example is not intended in any way to belittle the statistical method, but merely to deny it the character of a universal master-key, which is often attributed to it.

4. EXAMPLE: THE GROWTH OF A POPULATION

To illustrate more clearly the difference between the two methods, let us consider a biological problem, that of the growth of a homogeneous population. Let p be the number of inhabitants of a given area at a time t, and let the composition of the population be compared at times t and $t + h$. The difference between $p(t + h)$ and $p(t)$ depends on:

1. The individuals born in that period $(t, t + h)$.
2. The individuals dying in the same period.
3. The individuals entering the area (immigrants).
4. The individuals leaving the area (emigrants).

If the interval h between the two times is not great, it may be assumed (and statistics confirm this), that

all these increases and decreases are proportional to h. On the other hand, the same common sense, supported by statistics, suggests that the number of births and deaths are proportional to p. Thus we may write:

No. of births in $(t, t + h) \simeq Nph$
No. of deaths in $(t, t + h) \simeq Mph$

where N and M are uncorrected co-efficients of birth-rate and mortality. As to emigration and immigration, these are also proportional to h, but their dependence on p is more complicated. If Ih and Eh be these increments, we get:

$$p(t + h) - p(t) = Nph - Mph + Ih - Eh$$

or, dividing by h

$$\frac{p(t + h) - p(t)}{h} = Np - Mp + I - E \qquad (1)$$

i.e., the average rate of increase of the population.

Proceeding to the limit as h approaches zero, we get

$$p'(t) = Np(t) - Mp(t) + I - E \qquad (2)$$

It may be pointed out that this step is not altogether justifiable, since p is essentially discontinuous. This is a condition of great significance, the neglect of which may lead to fallacious results. It does not do so when p is sufficiently large, but when p is small, or when the density of the population is small, special precautions must be taken in order that the calculated results may agree with reality.

The co-efficients N, M, I, and E are not constant but depend on both p and t. In fact, the uncorrected fertility N decreases and the uncorrected mortality M

increases with growth of the population. Of all the hypotheses on the nature of this dependence the linear form

$$N = n - \nu p, \qquad M = m + \mu p \qquad (3)$$

is the simplest and is the most in accordance with the statistical data. Putting the above expressions (3) into equation (2) we get

$$p'(t) = \varepsilon p(t) - h p^2(t) + I - E \qquad (4)$$

where

$$\varepsilon = n - m \quad \text{and} \quad h = \nu + \mu \qquad (5)$$

We shall call ε the co-efficient of increase, h the limiting co-efficient, n the intrinsic co-efficient of fertility, ν the limiting co-efficient of fertility, m the intrinsic co-efficient of mortality, μ the complementary co-efficient of mortality, and all the co-efficients in biological equations of the type of equation (4) the vital co-efficients. We shall see later that very simple hypotheses on emigration and immigration enable us to replace E and I by appropriate functions of p.

The vital co-efficients depend on all the factors that can influence a population, climate, area colonized, food, social organization, etc. Further, it often happens that the simple relations of equation (3) are not always verified, yet at the same time equation (4) may be accurate while equation (3) is not. In other cases more complex hypotheses are necessary, and equation (2) assumes a more complicated form. It will be shown later that the simple form of equation (4), with all the consequences that follow from it, conveniently expresses a very considerable number of biological facts.

5. HISTORICAL REMARKS

We conclude this chapter with a few historical remarks. Natural science has used the statistical method for a long time, but it is to the great English scholar Karl Pearson that we owe a complete revision of the method and the foundation of a new science—biometry.

Equation (4) was first given by Verhulst in 1845 in discussing an isolated population. Since the works of Verhulst special biological problems have from time to time been investigated by the analytical method, but it is to Lotka, and independently to Volterra, that the honour belongs of having systematically applied the method to more general problems. The work of Lotka in physical biology has inaugurated a bio-mathematical movement in Anglo-Saxon countries. The brilliant work of Volterra, so fertile in mathematical suggestion, has started a similar movement on the continent of Europe. Pearl's half theoretical, half experimental researches on the laws of population growth have provided the basis of modern demography. J. B. S. Haldane's very important contribution to the mathematical theory of Natural Selection should also receive mention.

CHAPTER II

SOME MATHEMATICAL IDEAS

IN this chapter we shall briefly consider some mathematical ideas that will be useful later.

1. FREQUENCY CURVES

Suppose that we have to study statistical data referring to any biological character, such as size in a group of animals. We subdivide the range between the smallest and the largest into a number of equal intervals and count the number of animals whose size falls within each of these divisions. These figures can be represented by a polygon of frequency in which the abscissae are the sizes and the ordinates are the numbers of animals included in the corresponding size-interval. This gives a polygon which for the best-known infusorians, Paramecium, has the characteristic form of Fig. 1.

FIG. 1.—FREQUENCY POLYGON: Size of Paramecium (after Jennings).

This polygon shows that the smallest and the largest individuals are rare, that the average size is the commonest, and that the polygon is to all intents and purposes symmetrical about a median line. This distribution can be represented by many curves, but for many reasons the Gaussian curve is chosen. Let l be the size, l_m the average size, N the total number of individuals and Δn the number whose size falls within the interval $(l, l + \Delta l)$. Then

$$\Delta n = \frac{N\sqrt{\pi}}{h} e^{-h^2(l - l_m)^2} \Delta l \qquad (1)$$

A frequency curve of this kind is completely determined by three parameters, of which the first, l_m, gives the position of the peak, the second, N, the total number of individuals, and the third, h, the distribution about the average. Law (1) is that of the distribution of chance errors about a mean. By supposing that the distribution of size verifies this law we implicitly admit that this biological character only obeys the law of chance, that is to say that the distribution of size about the average l_m is governed by no special factor and that the statistical material is homogeneous.

In the special case of Paramecium these conclusions are not true. The material is heterogeneous, for Jennings' statistics do not distinguish between individuals of different ages, and age is a factor which certainly influences the parameters of curve (1). In fact, curve (1) more or less resembles the polygon of Fig. 1, but does not represent it satisfactorily, and one gets the impression that a curve of the type

$$\Delta n = A_1 e^{-h_1^2(l - l_1)^2} \Delta l + A_2 e^{-h_2^2(l - l_2)^2} \Delta l + A_3 e^{-h_3^2(l - l_3)^2} \Delta l$$

would be preferable. Consequently it is always neces-
sary to standardize the material, that is to say to study
the distribution of characters among individuals of the
same age, the same race,
etc. In many cases the
heterogeneous nature of
the material is expressed
in the frequency polygon
itself, in the form of
several peaks. This is true
of a mixed population
composed of two forms
of Paramecium (Fig. 2).
Peak α corresponds to
Paramecium aurelia, and
peak A to *Paramecium
caudatum*. In this case the distribution can be
represented by the curve

FIG. 2.—FREQUENCY POLYGON:
Body-length of Paramecium
(after Jennings).

$$\Delta n = A_1 e^{-h_1{}^2(l-l_1)^2} \Delta l + A_2 e^{-h_2{}^2(l-l_2)^2} \Delta l \qquad (2)$$

Frequency curves are often found with two or three
peaks, but it is not always easy to ascertain the reason
for the complexity. Sometimes it is a difference in
age, as in birds with a seasonal diet; the age-groups
are separated by a considerable interval and the average
size of the young is not the same as that of the adults.
Sometimes it is sex dimorphism. In some cases the
activity of predatory foes selectively destroys the
individuals of particular size- or age-groups and so
creates an apparent heterogeneity in a homogeneous
population. Again, features of the environment, such
as temperature or humidity, act upon biological char-
acters and if the statistical material reflects the whole

of the results on a homogeneous population the frequency curve may have several peaks.

From a mathematical point of view, the operation of dissecting a frequency curve with several maxima, that is to say the determination of all the parameters in an expression of type (2) presents considerable difficulty and uncertainty even in the simplest cases. This uncertainty is further increased by the fact that the frequency curve of Gauss is not the only one: it corresponds to the simplest schemata of probability only. Such a schema of probability is a vessel filled with balls of two or of different colours. One ball is taken from the vessel and is then returned to it so that the conditions in subsequent tests shall be unchanged. In such a series of experiments the distribution of deviations from the mean corresponds to law (1). Hence Gauss's law is valid only when the tests are completely independent of one another.

Other methods of conducting the experiment can be suggested, the balls not being returned to the vessel, or being returned according to certain more or less complex rules which would produce a dependence between successive tests, or replacement may be delayed, conditioned, etc.

In this way frequency curves differing from (1) are obtained. Pearson, in studying the distribution of biological characters, realized the impossibility of representing them all by curve (1) or its variations. He introduced a new group of frequency curves by generalizing the differential equation of the curve

$$\phi = A e^{-h^2(x - x_m)^2} \qquad (1')$$

Taking the derived logarithm of (1') we get the equation

$$\frac{\phi'}{\phi} = 2h^2(x_m - x) = \frac{x_m - x}{\alpha_0} \tag{3}$$

This equation shows that the relative growth of ϕ is proportional to the difference $(x_m - x)$. Pearson assumed that the co-efficient of proportionality α_0 is not constant, and substituted for equation (3)

$$\frac{\phi'}{\phi} = \frac{x_m - x}{\alpha_0 + \alpha_1 x + \alpha_2 x^2} \tag{4}$$

There are several arguments in favour of this generalization; it is sufficient to say that urn schemata can be constructed to reproduce the majority of Pearson's frequency curves. The curves resulting from the solution of equation (4) have very different appearances and can account for several distributions where curve (1) fails to do so. Further, the many factors determining size and other biological characters are related to, and dependent on, each other. Hence all the curves that analysis produces must be admitted on equal footing. For each curve schemata of probability can be found, justifying its use for the representation of distribution of characters. For a mathematical naturalist this implies freedom of choice and the end of the monopoly of type (1).

2. EVOLUTION OF A FREQUENCY CURVE

A frequency polygon may vary with time—for example, it may vary with age if one is studying the distribution of a character in a homogeneous population. This polygon may be represented by a frequency

curve of a type determined by co-efficients varying with age. Suppose, for instance, that the character studied is human stature, and that we have frequency polygons for each age of human life. We can represent these polygons by Gaussian curves and calculate for each age the average stature, the number of individuals of this age and the dispersion. All these parameters have a real biological meaning and the study of their variation with age gives valuable results.

However, this procedure will not serve in every case. It often happens that the frequency curve of a certain type can represent only a part of the development of a population, and it is necessary to look for another expression. In other cases the existence of a simple causality determines the distribution and makes statistical representations valueless. The following is a biological example in which this condition obtains.

The females of a species of moth *Lithocolletis populifoliella* Tr. deposit their eggs on the leaves of poplars. Poléjaeff has studied the relation between the number of eggs laid on a leaf and the area of the leaf, and also the relation between the number and the mortality of the caterpillars on a leaf. Fig. 3 gives the three successive stages of contamination of the leaves by these moths. Let f be the area of a leaf and p the number of eggs laid on a leaf. Fig. 3 shows that on three successive ovipositions—June 13, June 17, June 21—the number of eggs per leaf is proportional to the area

$$p = Af, \qquad (5)$$

but A, the co-efficient of utilization, varies with the date—

Date	June 13	June 17	June 21
A . .	·42	·91	1·28

There is a certain slowing down in the rate of utilization of the leaves.

How are these facts to be interpreted? The first
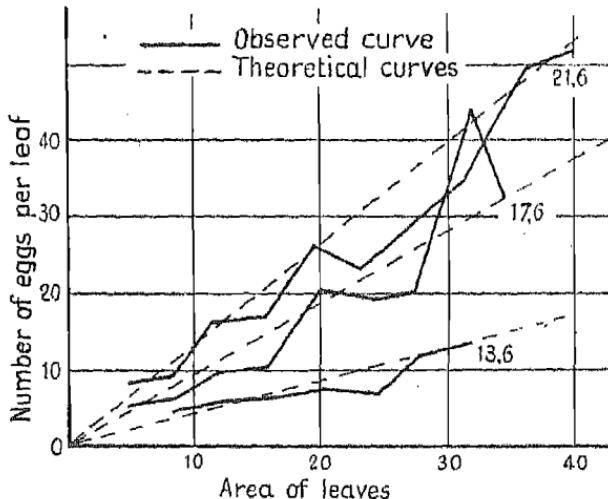
FIG. 3.—INFECTION OF POPLAR LEAVES BY MOTHS

explanation, suggested by equation (5) is the existence of a relation between the number of eggs laid and the path taken over the leaf by the insect during oviposition. This obvious explanation is not in accordance with the fact that the moth does not lay more than two eggs a day, while on the first day of laying the number of eggs varies from 4 to 13. Hence the eggs on any one leaf have not all been laid by a single female. Moreover, Fig. 3 shows that the number of

small leaves used increases between the first and fifth days of oviposition. The ratio between the maximum and minimum area per egg decreases, as the following figures show—

DATE	JUNE 13	JUNE 17	JUNE 21
Max. area .	6·80	2·30	1·10
Min. area .	·40	·20	·25
$\dfrac{\text{Max. area}}{\text{Min. area}}$.	17	11·5	4·4

On the ninth day of egg-laying the utilization of the leaves is greater than on the first day, but is not complete. Poléjaeff sees in these figures a sign of preference for large leaves. In my opinion the moth tries above all to ensure a sufficient food supply for its caterpillars: on the first day of oviposition it visits large leaves, avoiding, as far as possible, leaves that are already occupied. On the following days eggs are laid wherever there is space available, with no preference for large or small leaves. The increasing difficulty in the search for an unoccupied area is expressed in the retardation of increase of the co-efficient of utilization A. From the insect's point of view this method of egg-laying is evidence of very bad adaptation. The presence of many caterpillars on one leaf facilitates epidemics, attracts parasites and predators, and creates many inconveniences for the caterpillars themselves. Chance plays a great part in the wanderings of these insects, but the final result is subordinated to a very simple causality.

3. CORRELATION AND CAUSALITY

Search for a causal bond between two phenomena is not easy. Galton has suggested a practical method

which is of service in certain cases. Suppose that observation gives two series of numbers

$$\left.\begin{array}{l} x_1, x_2, \ldots, x_n \\ y_1, y_2, \ldots, y_n \end{array}\right\} \quad (6)$$

between which a relation is suspected of the nature

$$F(x, y) = 0 \tag{7}$$

Suppose that the function $F(x, y)$ be expanded according to Taylor's theorem—

$$F(x, y) = a_0 + a_1 x + a_2 y + \ldots \tag{8}$$

and that terms above the first order are negligible. Equation (7) can then be re-written

$$a_0 + a_1 x + a_2 y = 0 \tag{9}$$

If this expression of the relation between x and y is permissible, the points

$$(x_1, y_1), \ (x_2, y_2), \ \ldots, \ (x_n, y_n)$$

cannot lie far from the straight line (9).

Imagine such a straight line and estimate the sum of the distances between it and the points (x_k, y_k)

$$E = \sum_{k=1}^{n} \frac{(a_0 + a_1 x_k + a_2 y_k)^2}{a_1^2 + a_2^2} \tag{10}$$

For simplicity, put $\quad X = \frac{1}{n} \sum_{k=1}^{n} x_k \quad Y = \frac{1}{n} \sum_{k=1}^{n} y_k$

$$A = \frac{1}{n} \sum_{k=1}^{n} x_k^2 \quad B = \frac{1}{n} \sum_{k=1}^{n} y_k^2 \quad C = \frac{1}{n} \sum_{k=1}^{n} x_k y_k$$

$$d = \frac{a_0}{\sqrt{a_1{}^2 + a_2{}^2}} \quad \cos \theta = -\frac{a_1}{\sqrt{a_1{}^2 + a_2{}^2}}$$

$$\sin \theta = -\frac{a_2}{\sqrt{a_1{}^2 + a_2{}^2}}$$

Equation (10) then becomes

$$E = \sum_{k=1}^{n} (d - x_k \cos \theta - y_k \sin \theta)^2$$

or $E = n(d^2 - 2Xd \cos \theta - 2Yd \sin \theta + A \cos^2 \theta$
$$+ 2C \cos \theta \sin \theta + B \sin^2 \theta) \qquad (10')$$

Seeking the values of d and of θ which make this expression a minimum, we get by equating to zero the derivatives of E in respect of d and θ

$$d - X \cos \theta - Y \sin \theta = 0 \qquad (11)$$

$$dX \sin \theta - dY \cos \theta + C \cos 2\theta - \frac{A - B}{2} \sin 2\theta = 0 \quad (12)$$

Equation (11) shows that the point (X, Y), the centre of gravity, of the points (x_k, y_k) lies on the line (8). Equation (12) gives the value of θ in terms of these points:

$$\tan 2\theta = \frac{2(C - XY)}{A - X^2 - B + Y^2}. \qquad (13)$$

Further, the minimum value of E satisfies the equation

$E^2 - En(A + B - X^2 - Y^2)$
$$+ n^2[(A - X^2)(B - Y^2) - (C - XY)^2] = 0 \qquad (14)$$

It can easily be shown that

$A \geqslant X^2; \ B \geqslant Y^2; \ (A - X^2)(B - Y^2) \geqslant (C - XY)^2$
and therefore we may write

$$r^2(A - X^2)(B - Y^2) = (C - XY)^2 \qquad (15)$$

in which the co-efficient r^2 is equal to or less than unity. Equation (14) becomes

$$E^2 - En(A + B - X^2 - Y^2)$$
$$+ n^2(1 - r^2)(A - X^2)(B - Y^2) = 0 \qquad (16)$$

This equation has two positive roots, of which the smaller gives the required minimum. Suppose that all the points (x_k, y_k) lie on the line (9). In this ideal case $E = 0$, but equation (16) shows that E can only disappear when

$$r^2 = 1.$$

Further, in the case of symmetrical distribution of the points (x_k, y_k) about the point XY we get

$$r^2 = 0$$

In all other cases r^2 is less than unity, and it is natural to use this co-efficient to measure the possibility of representing a group of points by a straight line. The co-efficient r is called the co-efficient of correlation.

The co-efficient of correlation is zero when it is impossible to represent the observations (6) by a straight line, but this does not mean that the magnitudes of x and y are independent: it simply means that the function $F(x, y)$ cannot be even approximately replaced by the linear expression (9). This important fact is often forgotten and it is always worth remembering.

4. Two Connected Series of which the Correlation is Zero

We give an example of two connected series of which the correlation is zero although the variables are not independent. Suppose that two biological variables are functions of the time t. Let ω be an interval of time during which the variables x and y have been

observed. The sums X, Y, A, B, and C may be replaced by the integrals

$$X = \frac{1}{\omega} \int_{t_0}^{t_0 + \omega} x \, dt, \quad Y = \frac{1}{\omega} \int_{t_0}^{t_0 + \omega} y \, dt,$$

$$A = \frac{1}{\omega} \int_{t_0}^{t_0 + \omega} x^2 \, dt, \quad B = \frac{1}{\omega} \int_{t_0}^{t_0 + \omega} y^2 \, dt, \quad C = \frac{1}{\omega} \int_{t_0}^{t_0 + \omega} xy \, dt.$$

Suppose next that x and y are periodic functions of time for the interval ω and that

$$C = XY \tag{17}$$

In this case the co-efficient of correlation is zero, however closely x and y may be united by a causal bond. This is what occurs in the case of a mixed population composed of two species one of which feeds on the other and where the densities of the populations of the two species are sufficiently small for the limiting terms in each species to be negligible. Let x be the number of the species preyed upon and y the number of predators. The variables x and y satisfy a system of differential equations

$$\left. \begin{array}{l} x' = \varepsilon_1 x - h_{12} xy \\ y' = -\varepsilon_2 y + h_{21} xy. \end{array} \right\} \tag{18}$$

The term $\varepsilon_1 x$ implies that in the absence of predators the first species will increase according to the Malthusian law

$$x = x_0 e^{\varepsilon_1 t};$$

the term $-\varepsilon_2 y$ implies that in the absence of food the second species will be driven to extinction according to the exponential law

$$y = y_0 e^{-\varepsilon_2 t};$$

the term $-h_{12} xy$ implies that each encounter between a predator and its prey is followed by destruction of

c

the latter; the term $h_{21}xy$ expresses the benefit which the predators gain from this. It will later be seen that a simple relation exists between x and y,

$$x^{\varepsilon_2}y^{\varepsilon_1}e^{-h_{21}x - h_{12}y} = \mathrm{H}, \tag{19}$$

which shows that x and y are periodic functions of t. Let ω be this period. Integration of equation (18) gives

$$\mathrm{X} = \frac{\varepsilon_2}{h_{21}}, \qquad \mathrm{Y} = \frac{\varepsilon_1}{h_{12}}, \qquad \mathrm{XY} = \mathrm{C} \tag{20}$$

or, in other words, the relation of equation (17) is verified and the co-efficient of correlation is zero, and nevertheless x and y may be connected by equation (19).

The case represented by equation (18) is not a special one, nor is it purely theoretical. Periodic or periodomorphic* oscillations are in fact observed in mixed populations and in this case it would be actually misleading to apply the method of correlation, with the formidable calculus that it requires, to the search for a dependence between biological variables that cannot be detected in this way. This does not mean that the method of correlation is wholly useless, but it greatly restricts its application and provides a further argument for the analytical method.

5. Systems of First Order Differential Equations

The following equation has been obtained for a homogeneous population:

$$p' = \varepsilon p - hp^2 + \mathrm{I} - \mathrm{E}. \tag{21}$$

Suppose that the terms I and E, which express immi-

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* By this term I describe oscillations that are not strictly periodic. I wish to avoid the terms *pseudo-periodic* and *quasi-periodic*, as these have been used for some time in a specialized sense.

gration and emigration, depend only on the function $p(t)$. Equation (21) may then be written

$$p'(t) = \phi[p(t)] \tag{22}$$

Similarly, in the case of a mixed population composed of different groups $p_1, p_2, \ldots, p_n$, these variables satisfy differential equations of the first order.

$$p_k' = \phi_k(p_1, p_2, \ldots, p_n) \quad (k = 1, 2, \ldots, n.) \tag{23}$$

In most cases the function ϕ_k is a polynomial of the second order in relation to the functions $p_1, p_2, \ldots, p_n$. Even with this simple hypothesis, equation (23) can be successfully resolved in a few simple cases only. Yet in the absence of a numerical solution, we must rest content with a qualitative study which can none the less give very interesting biological results.

Consider the values

$$p_1 = a_1, \ p_2 = a_2, \ldots, \ p_n = a_n \tag{24}$$

which solve the algebraic equation

$$\phi_1 = 0, \ \phi_2 = 0, \ldots, \ \phi_n = 0 \tag{25}$$

If $p_1, p_2, \ldots, p_n$ are given initial values equal to (24), these functions remain constant and the mixed population does not change; system (24) then represents a stationary state or a state of equilibrium. Several equilibrium states may exist and it is essential to distinguish those that are stable from those that are not.

Stability may be variously defined. We may speak of stability when small variations in the co-efficients are followed by only small variations in the results. The study of this stability will be kept for a later chapter. We may speak of stability when in the neighbourhood of a stationary state (24) small variations in initial values lead to solutions tending, when $t \to \infty$, towards the values (24). This stability will be considered here.

Suppose p_1, p_2, . . . , p_n to be the initial values in the state of equilibrium (21) and let

$$p_1 = a_1 + \xi_1, \, p_2 = a_2 + \xi_2, \, . . . , \, p_n = a_n + \xi_n$$

where ξ_1, ξ_2, . . . , ξ_n are of very small magnitude, so that their squares, products, etc., are negligible. Substitute these values in equations (23). Since the functions ϕ_1, ϕ_2, . . . , ϕ_n are polynomials in relation to p_1, p_2, . . . , p_n we may write, taking equation (25) into account

$$\phi_k(p_1, \, p_2, \, . . . , \, p_n) = \sum_{m=1}^{n} \frac{\partial \phi_k}{\partial a_m} \, \xi_n$$

and equations (23) become

$$\xi'_k = \sum_{m=1}^{n} \frac{\partial \phi_k}{\partial a_m} \, \xi_m \qquad (k = 1, 2, \, . . . , \, n) \qquad (26)$$

These equations can be resolved into exponential functions. Suppose that

$$\xi_k = A_{k_1} e^{\mu_1 t} + A_{k_2} e^{\mu_2 t} + \, . . . \\ + A_{k_n} e^{\mu_n t} \qquad (k = 1, 2, \, . . . , \, n) \qquad (27)$$

The exponents μ_1, μ_2, . . . , μ_n satisfy the algebraic equation of the nth order.

$$\left. \begin{array}{cccc} \dfrac{\partial \phi_1}{\partial a_1} - \mu, & \dfrac{\partial \phi_1}{\partial a_2}, & \cdots & \dfrac{\partial \phi_1}{\partial a_n} \\[2mm] \dfrac{\partial \phi_2}{\partial a_1}, & \dfrac{\partial \phi_2}{\partial a_2} - \mu, & \cdots & \dfrac{\partial \phi_2}{\partial a_n} \\[2mm] \cdots & \cdots & & \cdots \\[2mm] \dfrac{\partial \phi_n}{\partial a_n}, & \dfrac{\partial \phi_2}{\partial a_2}, & \cdots & \dfrac{\partial \phi_n}{\partial a_n} - \mu \end{array} \right\} = 0 \qquad (28)$$

This equation, known as the *characteristic* or *secular equation*, has n roots, μ_1, μ_2, . . . , μ_n.

These roots may be real or imaginary. If they are all negative or with negative real parts, the equilibrium is stable, for the fluctuations (27) tend towards zero. If only one of the exponents is positive or zero, or with a real part positive or zero, the equilibrium is unstable.

Consider, as an example, the case in which $n = 2$. Equation (28) becomes

$$\left.\begin{array}{cc} \dfrac{\partial \phi_1}{\partial a_1} - \mu, & \dfrac{\partial \phi_1}{\partial a_2} \\[2ex] \dfrac{\partial \phi_1}{\partial a_1}, & \dfrac{\partial \phi_2}{\partial a_2} - \mu \end{array}\right\} = 0$$

or $\qquad\qquad \mu^2 - \mu C + D = 0 \qquad\qquad$ (29)

where $C = \dfrac{\partial \phi_1}{\partial a_1} + \dfrac{\partial \phi_2}{\partial a_2} \quad D = \dfrac{\partial \phi_1}{\partial a_1}\cdot\dfrac{\partial \phi_2}{\partial a_2} - \dfrac{\partial \phi_1}{\partial a_2}\cdot\dfrac{\partial \phi_2}{\partial a_1}.$ (30)

When $C < 0$, $D > 0$, $E = C^2 - 4D > 0$, there is a node, that is to say the two solutions of the characteristic equation are negative and the point (p_1, p_2) approaches (a_1, a_2), following an arc (Fig. 4A).

When $C < 0$, $D > 0$, $E = C^2 - 4D < 0$, there is a focus, that is to say the roots of equation (29) are partly real and negative, and the point (p_1, p_2) tends towards (a_1, a_2), describing a spiroidal curve (Fig. 4B).

When $C = 0$, $D > 0$, $E < 0$ there is a cycle, that is to say the two solutions of equation (29) are purely imaginary and the point (p_1, p_2) describes a closed curve round the point (a_1, a_2), (Fig. 4C). This is what happens in the case considered in the preceding section.

Let us return to the general case. Equations (25) have several sets of solutions of type (24) and each of these corresponds to a stationary state. Some of them

are composed of negative or of complex expressions and hence have no interest here; the others may be stable or unstable. In the case in which there are several compatible stable states the final end of the biological system depends on the initial values $p_1(0)$, $p_2(0)$, ..., $p_n(0)$ in the sense that each final state is surrounded by a region under its influence and if the initial state is in one of these regions, the corresponding final state is the limit.
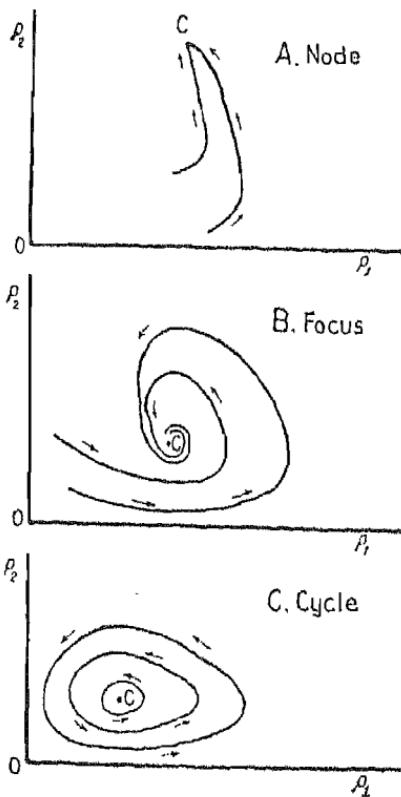
FIG. 4.—CURVES OF RELATIVE GROWTH FOR TWO GROUPS, p_1 AND p_2

The variables p_k are generally positive. What happens if one of them vanishes? This implies that one of the groups composing the mixed population is extinct. For its reappearance new circumstances are essential, for example, an immigration or the hatching of some eggs which might have remained hidden. If there is no reason for the reappearance of a lost group, equations (23) must be revised to determine the effect of the

extinction of the group. It is not sufficient to replace by zero the variable that corresponds to the lost group for it may have an indirect influence on the vital co-efficients of the other groups in the population.

If the numbers of one group approximate to zero, equations (23) must be handled cautiously, for biological variables are essentially discontinuous, and the reduction of a group to a few individuals may be equivalent to its disappearance, which equations (23) do not provide for. On the contrary, biological equations, in order to be logical, must be concerned with large numbers, and for small numbers the form of these equations would be different.

Other comments will be made in the examination of concrete biological problems.

6. BIOLOGICAL DIFFERENTIAL EQUATIONS

We conclude this chapter by some consideration of biological differential equations. In almost every case that will be studied these equations belong to the type

$$p'_k = \alpha_k + \sum_{s=1}^{n} \varepsilon_{ks} p_s - p_k \sum_{s=1}^{n} h_{ks} p_s$$

$$(k = 1, 2, \ldots, n) \qquad (31)$$

The term α_k expresses the constant sum of emigration and immigration. The co-efficients ε_{kk} almost always represent the intrinsic multiplication of the group p_k. The term $\varepsilon_{ks} p_s$, in which $k \neq s$, corresponds to possible transfers from one group to another, as for example in the case of a species divided into age-groups. The term $h_{kk} p^2_k$ represents the limiting action on the

group p_k of all limiting factors save the action of other groups in the same population. The term $h_{ks}p_kp_s$ represents the interaction between the groups. It will be seen that other interpretations of these groups are possible.

These equations produce 2^n separate points, which represent stationary states. We are here concerned with a fairly common special case, that of an isolated system composed of a certain number of groups, without the possibility of passage from one to the other. In this case we have the equations of Volterra:

$$p'_k = p_k \left(\varepsilon_k - \sum_{s=1}^{n} h_{ks}p_s \right) \quad (k = 1, 2, \ldots, n) \quad (32)$$

The 2^n equilibrium states always remain theoretically possible. It is easy to enumerate them all. First we have the state

$$P_1 = 0, P_2 = 0, \ldots, P_n = 0 \tag{33}$$

which is only stable if all the co-efficients of increase are negative.

$$\varepsilon_k < 0 \quad (k = 1, 2, \ldots, n). \tag{34}$$

Then there are n stationary states of the type

$$P_k = \frac{\varepsilon_k}{h_{kk}}, P_1 = 0, \ldots, P_{k-1} = 0, P_{k+1} = 0,$$
$$\ldots, P_n = 0 \tag{35}$$

These equations imply that all groups save one disappear. Some of these states may be negative and of no interest to us. A state of type (35) is stable if the inequalities

$$\varepsilon_k > 0, \ h_{kk} > 0,$$
$$\varepsilon_s h_{kk} < h_{sk}\varepsilon_k, \ (s = 1, 2, \ldots, k-1, k+1, \ldots, n) \tag{36}$$

are satisfied. These n states may be compatible with each other. Consider, for example, two states of the order k and l. We may have simultaneously

$$\varepsilon_k > 0,\ h_{kk} > 0,\ \varepsilon_s h_{kk} < h_{sk}\varepsilon_k \quad (s \neq k)$$
$$\varepsilon_l > 0,\ h_{ll} > 0,\ \varepsilon_s h_{ll} < h_{s'l}\varepsilon_l \quad (s' \neq l)$$

It follows that

$$\varepsilon_l h_{kk} < h_{lk}\varepsilon_k$$
$$\varepsilon_k h_{ll} < h_{kl}\varepsilon_l$$

and therefore that

$$h_{kk}h_{ll} < h_{lk}h_{kl}$$

These inequalities are not contradictory. On the other hand, state (35) is incompatible with state (33).

Then there are $\dfrac{n(n-1)}{2}$ stationary states of the type

$$P_1 = \frac{\varepsilon_1 h_{22} - \varepsilon_2 h_{21}}{h_{11}h_{22} - h_{12}h_{21}}, \quad P_2 = \frac{\varepsilon_2 h_{11} - \varepsilon_1 h_{12}}{h_{11}h_{22} - h_{12}h_{21}}, \quad (37)$$
$$P_3 = 0,\ \ldots,\ P_n = 0.$$

We may continue in this way and obtain all the equilibrium states of the system. Without pausing over the stability and the compatibility of these states, we shall only mention the equilibrium state in which all the groups of the system share. This state is defined by the linear equations

$$\varepsilon_k = \sum_{s=1}^{n} h_{ks} P_s \quad (k = 1, 2, \ldots, n) \tag{38}$$

This state is stable if the secular equation (28) has all its roots ($\mu_1, \mu_2, \ldots, \mu_n$) negative or with negative real parts.

CHAPTER III

LIFE AND ENVIRONMENT

1. Circulation of Organic Matter

Let us consider the life process as a whole, and in its relations with inorganic matter. Such matter exists in several forms, but the atmosphere is the chief source from which living organisms absorb the elements necessary for the formation of complex compounds and of living matter. The process of the assimilation of the absorbed matter consists of several stages. Plants absorb atmospheric carbon, converting the carbon dioxide into starch and liberating the oxygen, and comparable to this are the organisms living in the sea which absorb carbon dioxide and convert it into chalk. Nitrogen is a more inert component of the atmosphere than oxygen or carbon dioxide; it is fixed by soil bacteria living symbiotically with certain plants. Thus nitrogen becomes available for further syntheses, ending in the formation of living matter. Other micro-organisms may be mentioned, which fix other elements necessary for the production of organic matter, as well as natural factors, such as thunderstorms, which facilitate the absorption of nitrogen by living organisms.

In spite of their variety, all these processes can be summarized in the form of simple differential equations, capable of supplying information as to the nature of the life process in its general relations with the inorganic world.

We may rapidly review the principal sources and ultimate destinations of each substance taking part in these reactions.

1. **Atmospheric Oxygen.** Owing to its chemical affinities, the oxygen of the air cannot be considered as one of the original constituents of the earth's atmosphere; it is rather the result of the activity of living organisms. It is evolved by plants in the process of the assimilation of atmospheric carbon, and absorbed by all living objects in respiration as well as in human industries. It is impossible to point to any source of this gas other than the chemical actions occurring in plants.

2. **Atmospheric Carbon.** This exists chiefly in the form of carbon dioxide. Its sources are volcanic action, respiration in animals and plants, decomposition of organic matter and inorganic oxidation of the earth's crust accompanied by the evolution of this gas. The causes of its removal are the absorption of carbon dioxide by plants and by chalk-producing organisms. An essential difference may be noted between the organisms that directly absorb carbon dioxide and those that only make use of carbon already assimilated.

3. **Atmospheric Nitrogen.** This is assimilated by organisms with the help of microbes in the soil and, perhaps, liberated in certain decomposition processes. It cannot be asserted that nitrogen is not evolved in some chemical reactions in the earth's crust, but there is no direct proof of this.

4. **Atmospheric Hydrogen.** The lower layers of the atmosphere contain only traces of this gas, which takes part only in infinitely small quantities in the life processes.

5. **Water.** Despite the importance of water in organic

life, the study of its circulation does not yield such useful information as does that of the atmospheric gases.

6. **Light Elements of the Earth's Crust.** These elements enter into the composition of living matter to a certain extent, but it would be premature to consider their circulation. The role of water as solvent, as carrier and as distributor is of fundamental importance in this, but the chief methods of circulation are far from obvious. Hence we are here confined to the mathematical study of the circulation of the three principal atmospheric gases.

2. THE CARBON-OXYGEN CYCLE

Consider first the particular problem of the carbon-oxygen cycle. Let

$x =$ the total weight of free atmospheric oxygen.
$y_1 =$ that of atmospheric carbon dioxide.
$y_2 =$ that of carbon dioxide dissolved in the sea.
$z =$ that of these substances in chalk-producing organisms.
$u =$ that of these substances in animals.
$v =$ that of these substances in plants.
$s =$ that of these substances dispersed through the earth's crust.

The relations between these variables can be summarized by a simple diagram (Fig. 5), or by the following differential equations:

$$x' = -\alpha_{13}u + (\alpha_{41} - \alpha_{14})v - \varepsilon_{15} \qquad (1)$$

$$y'_1 = \alpha_{32}u - (\alpha_{24} - \alpha_{42})v + \varepsilon'_{52} \qquad (2')$$

$$y'_2 = \varepsilon''_{52} - \gamma z y_2 \tag{2''}$$

$$u' = -(-\alpha_{13} + \alpha_{32} + \alpha_{35})u + \beta uv \tag{3}$$

$$v' = (\alpha_{14} - \alpha_{41} + \alpha_{24} - \alpha_{42} - \alpha_{45})v - \beta uv \tag{4}$$

$$s' = \alpha_{35}u + \alpha_{45}v + \alpha_{65}z - \varepsilon'_{52} - \varepsilon''_{52} + \varepsilon_{15} \tag{5}$$

$$z' = -\alpha_{65}z + \gamma z y_2 \tag{6}$$

The structure of these equations is very simple. Each term corresponds to one of the arrows in Fig. 5.
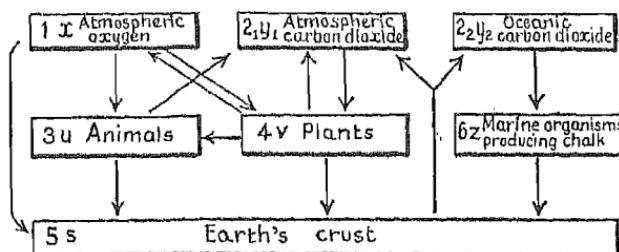
FIG. 5. CIRCULATION OF OXYGEN AND CARBON

Thus equation (1) shows that oxygen is consumed by the respiration of animals $(-\alpha_{13}u)$, and of plants $(-\alpha_{14}v)$, by inorganic oxidations of the earth's crust $(-\varepsilon_{15})$, and that it is liberated in the process of assimilation by plants. Equation (2') shows that the atmosphere receives the carbon dioxide evolved by animals $(\alpha_{32}u)$ and plants $(\alpha_{42}v)$ in the processes of respiration and decomposition of living matter, and that plants assimilate carbon dioxide $(-\alpha_{24}v)$: the term ε'_{52} represents what the atmosphere receives as liberated carbon dioxide, from volcanic eruptions and other chemical reactions in the earth's crust. Human industrial activity, which is rapidly destroying mineral sources of energy, is wholly neglected: in a few centuries these resources will be brought to nothing, and mankind

will have to seek other supplies of energy. The carbon
dioxide set free during this interval will be distributed
between the atmosphere and the sea water, and hence
our equations can be applied without the introduction
of supplementary terms; it is enough to replace the
numerical co-efficients by others more closely corre-
sponding to the partial pressure of atmospheric carbon
dioxide.

Equation $(2'')$ refers to the hydrosphere. The total
weight of carbon dioxide dissolved in the ocean is
thirty to forty times greater than that in the atmo-
sphere. To simplify these equations it is assumed that
this proportion does not vary and that the ocean
receives, through the intervention of the atmosphere,
a constant amount, ε''_{52}, of carbon dioxide supplied
by the earth's crust; the term $(- \gamma z y_2)$ represents
dissolved carbon dioxide absorbed by marine chalk-
producing organisms.

In equation (3) the terms $(\alpha_{13}u, - \alpha_{32}u)$ represent
the amounts that animals add to or extract from the
atmosphere; the term βuv shows that animals live at
the expense of plants and that process is regulated
by the so-called principle of encounters between pre-
dators and victims; the term $(- \alpha_{35}u)$ represents the
fertilization of the soil by the products of animal
metabolism.

Equations (4) to (6) do not differ in their mode of
construction from the above.

The most difficult problem, and one that is not
exactly represented by the equations $(2')$ and $(2'')$ is
that of the relation between atmospheric and oceanic
carbon dioxide. According to Schloesing, the masses
of oceanic water control the carbon dioxide in the sense

that the water loses carbon dioxide when the pressure of that gas in the atmosphere decreases, and absorb it in the reverse circumstances. This action ensures a degree of constancy in the co-efficients α_{32}, α_{24}, α_{42}, and consequently in the co-efficients α_{13}, α_{14}, α_{41}, but makes uncertain the values of ε'_{52} and ε''_{52}. As for oxygen, these co-efficients are not invariable, and depend on the pressure of this gas in the atmosphere, but the weight of atmospheric oxygen is sufficiently great to ensure relative constancy of α_{32}, α_{24}, α_{42}, α_{13}, α_{14}, and α_{41}. Thus the assumption of these constant co-efficients does not distort the truth very much, and the conclusions drawn from equations (1) to (6) remain valid.

It should be noticed that each term appears twice in these equations, once with a positive and once with a negative sign. Hence, on adding these equations we get:

$$x' + y'_1 + y'_2 + u' + v' + s' + z' = 0 \qquad (7)$$

and therefore

$$x + y_1 + y_2 + u + v + s + z = M \qquad (8)$$

which expresses the commonplace of the constancy of the weight of the globe.

Equations (1) to (6) may be arranged in three groups:

1. The variables x, y, and s do not occur on the right-hand side. Thus equations (1), (2'), and (5) enable us to calculate these variables when all the others are known.

2. Equations (2'') and (6) contain only two variables, y_2 and z.

3. Similarly, equations (3) and (4) contain only the

two variables u and v. Starting with equations (3) and (4), we may write:

$$u' = u(-\lambda + \beta v) \text{ and } v' = v(\mu - \beta u) \tag{9}$$

where $\qquad\qquad \lambda = \alpha_{32} + \alpha_{35} - \alpha_{13}$

and $\qquad \mu = \alpha_{14} - \alpha_{41} + \alpha_{24} - \alpha_{42} - \alpha_{45}$

The parameter λ is positive, for in the absence of plants animals cannot exist; the parameter μ is positive, for in the absence of animals plants develop almost without hindrance.

Equations (9) are only special cases of equation (18) of Chapter II, and equation (19) of Chapter II then becomes

$$u^\mu v^\lambda = He^{\beta u + \beta v} \tag{10}$$

where H is a constant depending on the original values of u_0 and v_0,

$$H = u_0{}^\mu v_0{}^\lambda e^{-\beta u_0 - \beta v_0}$$

Time does not enter explicitly into equation (10). To each positive value of H not exceeding a certain limit there corresponds in the graph of the variables (u, v) a closed curve (Fig. 4, (iii)) which is not cut by the analogous integral curves. This implies that u and v are periodic functions of the time t. Let ω represent the period, and let

$$u_0 = \frac{\mu}{\beta} \text{ and } v_0 = \frac{\lambda}{\beta}$$

be the co-ordinates of C, the common centre of all the curves (10). This period depends not only on the co-efficients λ, μ, and β, but also on the constant H; its value is zero when $u_0 = u_0$ and $v_0 = v_0$, and infinite

when $H = 0$. It has already been seen that the mean values of u and v are equal to u_0 and v_0.

$$\frac{1}{\omega} \int_0^\omega u \,.dt = u_0 = \frac{\mu}{\beta} \text{ and } \frac{1}{\omega} \int_0^\omega v \,.dt = v_0 = \frac{\lambda}{\beta} \quad (11)$$

This is a purely imaginary periodicity, for equations (9) are not true to a first approximation, and the vital co-efficients are not constant, but vary slowly. Actually this imaginary periodicity corresponds to a real phenomenon, to the rather irregular but periodomorphic fluctuations through which the system (u, v) passes and which might be confounded with periodic oscillations when the observations are not spread over a sufficiently great interval of time. The curve representing (u, v) may have cusps, which correspond to critical occasions, and limits, which correspond to relatively stationary conditions. In any case, it is seen that, apart from external factors, which may disturb the equilibrium (volcanic activity, glaciation, etc.) the actual structure of the organic world must produce a longer or shorter series of oscillations. The disappearance of these oscillations, owing to the adaptation of the organic world to a new set of circumstances, leads to a new stationary state, to a new stability which is never permanent.

Consider now equations (2″) and (6), which may be written more simply, omitting the indices:

$$y' = \varepsilon - \gamma zy, \qquad z' = -\alpha z + \gamma zy \qquad (12)$$

The action proceeds towards a stable stationary condition

$$y_0 = \frac{\alpha}{\gamma} \qquad z_0 = \frac{\varepsilon}{\alpha} \qquad (13)$$

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The word 'stable' must be interpreted in the sense that the state (13) can be maintained for a longer or shorter time, but it is certain that the co-efficients of equation (12) vary and that the state (13) varies with them.

Suppose that until a moment t_0 the volcanic effect is weak, so that*

$$\varepsilon\beta \ll 4\alpha^2$$

and that the stationary condition of equation (13) is almost reached. Suppose further that from this moment until a moment t_1 a period of volcanic activity occurs with an average effect E far greater than ε.

$$\mathrm{E} \gg \varepsilon.$$

Equilibrium is disturbed and the system (y, z) tends towards a new equilibrium state

$$\mathrm{Y}_0 = \frac{\alpha}{\gamma} = y_0 \qquad \mathrm{Z}_0 = \frac{\mathrm{E}}{\alpha} \gg z_0$$

Suppose that this state is almost reached at the time t_1. It is apparent that the new ultimate mass of oceanic carbon dioxide, Y_0, is equal to the original mass y_0, but the total mass of marine chalk-producing organisms has increased.

Assume that after this recrudescence of volcanic activity, normal relations are re-established, and that for $t > t_1$ the effect of carbon dioxide is again equal to ε. The state (y, z) tends to the original condition of equilibrium (13), describing decreasing spirals. This process is at first almost periodic, and the masses of carbon dioxide contained in the ocean and the atmosphere pass through a series of maxima and minima.

* $\ll$ = is much less than, $\gg$ = is much more than.

The same is true of the total mass of marine chalk-producing organisms, and in consequence terrestrial organisms are experiencing a critical occasion.

The co-efficients of equation (12) can be approximately calculated. Volcanoes and other internal sources evolve on the average 10^8 metric tons of carbon dioxide in a year. The total mass of living marine organisms is of the order of 10^{14} metric tons and it may be assumed that the mass of chalk-makers is of the order of 10^{13} metric tons. On the other hand, the mass of carbon dioxide dissolved in the ocean is 10^{14} metric tons. Thus we get:

$$\varepsilon = 10^8, \; y_0 = 10^{14}, \; z_0 = 10^{13}, \; \alpha = 10^{-5}, \; \gamma = 10^{-19}$$

These values practically verify the inequality

$$\varepsilon\beta \ll 4\alpha^2$$

necessary for the establishment of periodomorphic oscillations after a disturbance of equilibrium.

Are any traces of such oscillations to be found? Perhaps the series of chalk deposits may be explained by this mechanism. It seems that the marine deposits of the Black Sea show a periodicity of the order of two to three thousand years. I have tried to relate these oscillations to the quaternary glaciations, but another periodic mechanism affords a better explanation of all the phenomena accompanying glaciation, as well as of the glaciations themselves.

We pass on to the consideration of equations (1), (2'), and (5). Suppose that the time is one of relative stability and that the stationary condition (13) is almost reached as far as pelagic organisms and dissolved carbon dioxide are concerned. Integrate equations

(1), (2′), and (5) in respect of t, from t to $t + \omega$, putting throughout

$$y_2 = \frac{\alpha_{65}}{\gamma} \qquad z = \frac{\varepsilon''_{52}}{\alpha_{65}}$$

We find that the average increments of x, y, and s are equal to:

$$\frac{x(t + \omega) - x(t)}{\omega} = -\alpha_{13}\frac{\mu}{\beta} + (\alpha_{41} - \alpha_{14})\frac{\lambda}{\beta} - \varepsilon_{15} \quad (14)$$

$$\frac{y_1(t + \omega) - y_1(t)}{\omega} = \alpha_{32}\frac{\mu}{\beta} + (\alpha_{42} - \alpha_{24})\frac{\lambda}{\beta} + \varepsilon'_{52} \quad (15)$$

$$\frac{s(t + \omega) - s(t)}{\omega} = \alpha_{35}\frac{\mu}{\beta} + \alpha_{45}\frac{\lambda}{\beta} - \varepsilon'_{52} + \varepsilon_{15} \quad (16)$$

The ultimate result, or at least the actual tendency of this process depends on the vital co-efficients. If these co-efficients are in agreement with certain inequalities that are easy to establish and which lend themselves to simple biological interpretations, the atmospheric gases will be in a state of rhythmical increase or decrease, according to the periodic oscillations. Suppose, for example, that

$$\alpha_{14} - \alpha_{41} < 0$$

which means that plants evolve more oxygen than they use in respiration and also that α_{13} and ε_{15} are small enough to ensure a positive sign for equation (14). In this case the quantity of free oxygen will be continuously increasing.

Suppose, again, that

$$\alpha_{42} - \alpha_{24} < 0$$

that is to say that plants absorb more carbon dioxide than they evolve in respiration, and also that α_{32} and ε'_{52} are small enough to ensure a negative sign for

equation (15). In this case atmospheric carbon dioxide will be continuously decreasing, save for the regulating action of the oceans, but this reserve itself will not be inexhaustible.

Other consequences which follow from equations (14) to (16) will not be considered.

3. The Nitrogen Cycle

The above results may be completed by a study of the circulation of nitrogen. To simplify matters, suppose that the micro-organisms able to fix atmospheric nitrogen live symbiotically with plants: this will not appreciably affect the results and will diminish the number of variables and of equations. Let

$x =$ the total weight of free atmospheric oxygen.

$y =$ the total weight of carbon dioxide in the atmosphere and the ocean.

$z =$ the total weight of free nitrogen.

$u =$ the total weight of these substances in animals.

$v =$ the total weight of these substances in plants.

$s =$ the total weight of these substances in the earth's crust.

The relation between these variables may be represented by the accompanying diagram (Fig. 6) or by the differential equations:

$$x' = -\alpha_{14}u + (\alpha_{51} - \alpha_{15})v \tag{17}$$

$$y' = \alpha_{42}u - (\alpha_{25} - \alpha_{52})v \tag{18}$$

$$z' = -\alpha_{35}v - \varepsilon \tag{19}$$

$$u' = -(\alpha_{42} + \alpha_{46} - \alpha_{14})u + \beta uv \tag{20}$$

$$v' = (\alpha_{15} - \alpha_{51} + \alpha_{25} - \alpha_{52} + \alpha_{35} - \alpha_{56})v - \beta uv \tag{21}$$

$$s' = \alpha_{35}u + (\alpha_{45} - \alpha_{65})v + \varepsilon \tag{22}$$

the formation of which is similar to that of the equations in the preceding section. Suppose, as before, that in the absence of plants the balance of animal life will be diminishing, giving,

$$\lambda = \alpha_{42} + \alpha_{40} - \alpha_{14} > 0.$$

Similarly,

$$\mu = \alpha_{15} - \alpha_{51} - \alpha_{52} + \alpha_{35} - \alpha_{50} > 0$$
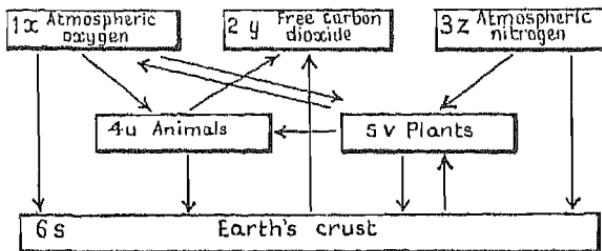
FIG. 6.—ATMOSPHERIC CIRCULATION

In these circumstances, equations (17) to (22) give results that do not differ from those of the previous paragraph. The variable z is always decreasing. Equations (20) and (21) have again periodic solutions. Adding the equations of the atmospheric gases, we get:

$$x' + y' + z'$$
$$= u(\alpha_{42} - \alpha_{14}) - (\alpha_{15} - \alpha_{51} + \alpha_{25} - \alpha_{52} + \alpha_{35})v - \varepsilon$$

Integrating this equation in respect of t from t to $t + \omega$, we get the average rate of disappearance of the atmosphere

$$\frac{x(t+\omega) + y(t+\omega) + z(t+\omega) - x(t) - y(t) - z(t)}{\omega}$$

$$= - \frac{\lambda \alpha_{50} + \mu \alpha_{40}}{\beta} - \varepsilon < 0$$

Hence the atmosphere, and the nitrogen in it, are continuously disappearing. The maximum speed of this disappearance can be estimated by simple considerations. The total mass of atmospheric nitrogen is of the order of 4×10^{15} metric tons. The earth's crust, at least in its upper layers, contains an amount of the same order of magnitude. Suppose that this combined nitrogen be of atmospheric origin, and that the process has so far lasted for 2×10^9 years, then the annual loss of atmospheric nitrogen does not exceed 2×10^6 metric tons, and by this computation the atmospheric nitrogen will not be exhausted before the passing of two thousand million years.

CHAPTER IV

GROWTH OF A POPULATION: THE LOGISTIC LAW

In this chapter the growth of an isolated population will be considered. Such a population closely follows the law of Verhulst, a fact that is confirmed both by observation and experiment.

1. DIFFERENTIAL EQUATION FOR AN ISOLATED POPULATION

In the first chapter we arrived at the differential equation

$$p'(t) = \varepsilon p(t) - h p^2(t) + I - E \qquad (1)$$

where ε is the co-efficient of multiplication, h the limiting co-efficient, I the co-efficient of immigration and E the co-efficient of emigration. The co-efficient of multiplication ε is the difference between fertility n and mortality m.

$$\varepsilon = n - m$$

For an isolated population with neither emigration nor immigration, equation (1) becomes

$$p'(t) = \varepsilon p(t) - h p^2(t) \qquad (2)$$

and in this form is known as the logistic equation. The co-efficient h is generally small compared to ε, and when $p(t)$ is small enough the second term of the

right-hand side may be neglected, which gives the Malthusian form of the population law

$$p'(t) = \varepsilon p(t) \tag{3}$$

whence $$p(t) = p(o)\varepsilon^{\varepsilon t} \tag{4}$$

One could give many biological examples of exponential growth according to this law; it happens whenever the necessities of life are sufficiently plentiful to abolish all competition between individuals. This occurs in the colonization of virgin territory so large that for a long time each colonist cannot 'see his neighbour's smoke.' As the population multiplies a sense of being cramped arises and the limiting term must be taken into consideration.

Example. The following is an example which shows that in optimum conditions fertility may remain constant for a long time. It deals with a small rodent, *Microtus arvalis* Pall, which multiplies with great rapidity. The following table gives the increase of the descendants of a single pair, mortality being neglected.

MONTHS	0	2	4	6	8	10	12	14
p observed .	2	5	16	20	40	109	200	283
p calculated	2	4·5	10	22	50	112	252	282

Calculated values are based on the formula $p = 2e^{\cdot 4t}$ The agreement is as close as possible, for pregnancy in these animals lasts three weeks, and the difference in time between the taking of a census and the birth of the young is often considerable.

Note on the Limiting Co-efficient. Another interpretation of the limiting term, differing from that given in

Chapter I, is possible. Numerical growth of a population may be impeded by competition between individuals, and the effect of this may be taken to be proportional to the number of encounters per unit of time. This number is proportional to $p^2(t)$, from which is derived the form of the limiting term $- hp^2(t)$ in equation (2). It may be noted that this form of the limiting term is too simple and takes no account of external limiting factors which have nothing to do with either encounters or competition. It is the whole of these factors that give its form to this term, and experience amply confirms the legitimacy of using it in the logistic law.

Chemical Interpretation. Equation (2) may be given a slightly different form—

$$\frac{dp}{dt} = hp\,(\omega - p) \text{ where } \omega = \frac{\varepsilon}{h} \qquad (5)$$

In this form the logistic equation expresses the progress of a reaction of which the velocity is proportional to the mass p of the products and to the mass $(\omega - p)$ of the reactants. This interpretation is meaningless as far as a population is concerned but it may be applied to the reactions in an organism.

2. THE LOGISTIC LAW

Write equation (5) in the form

$$\varepsilon dt = \frac{\omega dp}{p(\omega - p)} = \left(\frac{1}{p} + \frac{1}{\omega - p}\right) dp$$

Integrating, we get, when $p_0 < \omega$

$$\varepsilon t = \log \frac{p(\omega - p_0)}{(\omega - p)p_0} \qquad (6)$$

and when $p_0 > \omega$

$$\varepsilon t = \log \frac{p(p_0 - \omega)}{(p - \omega)p_0} \tag{6'}$$

These formulae give the logistic law of population-growth:

$$p = \frac{\omega p_0}{p_0 + (\omega - p_0)e^{-\varepsilon}} \tag{7}$$

The limit of p as $t \to \infty$ is equal to ω whatever the initial value of p_0; when $p_0 < \omega$, p increases to ω, and when $p_0 > \omega$, p decreases to ω.

When $p_0 < \dfrac{\omega}{2}$, curve (7) passes through a point of inflexion at

$$t = \frac{1}{\varepsilon} \log \frac{\omega - p_0}{p_0}$$

where the value of p is $\dfrac{\omega}{2}$, and when $\dfrac{\omega}{2} < p_0$ the maximum value does not exist.

The fundamental conclusion is therefore : *an isolated population tends towards a limit which only depends on the vital co-efficients; it is independent of the initial value of p_0.* This conclusion is only valid if the whole of the factors determining the vital co-efficients remain unchanged. These co-efficients depend on the neighbourhood occupied, on its resources, on its stage of mechanical development, and on the social organization of the population.

The United States. It is interesting to find that the logistic law

$$p = \frac{197,273,000}{1 + e^{-\cdot03134\,(t-1913\cdot25)}} \tag{8}$$

closely expresses the population of the United States. This is shown by Fig. 7 and the following table:

Year	p Observed	p Calculated	Year	p Observed	p Calculated
1790	3.9×10^6	3.9×10^6	1870	38.7×10^6	39.4×10^6
1800	5.3	5.3	1880	50.3	50.2
1810	7.2	7.2	1890	63.1	62.8
1820	9.6	9.8	1900	76.1	76.9
1830	12.9	13.1	1910	92.3	92.0
1840	17.1	17.5	1920	106.5	109.4
1850	23.2	23.2	1930	123.2	123.9
1860	31.5	30.4			

The agreement is almost baffling. Since 1790 the United States have waged five major wars, conquered new territory, colonized vast spaces, developed a
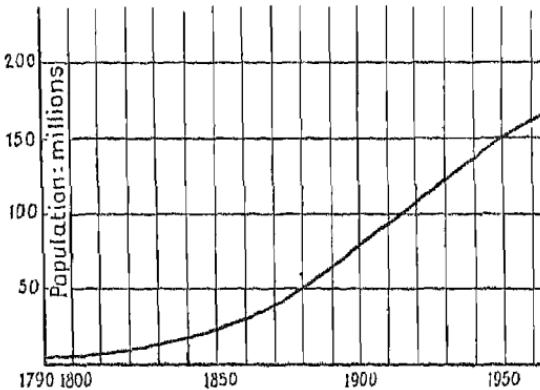
FIG. 7.—EXAMPLE OF A LOGISTIC POPULATION
Growth of Population in the United States.

formidable industrial organization, and have received and absorbed a mass of emigrants from all parts of the world, yet, in spite of all this, the logistic law closely expresses the growth of the population. It is seen that the point of inflexion at which accelerating growth gave place to diminishing growth was only passed in

1914 and that a state of saturation is a long way ahead. At the moment the population density is only 20 persons per square kilometre, which is still far below the European saturation-point.

France and Belgium. As far as European countries are concerned, Verhulst in 1845 calculated the conditions of saturation for France and Belgium. For Belgium he prophesied a maximum population of 6,600,000, and for France about forty millions. The present population of Belgium is (1930) 8,092,000, corresponding to 266 persons per square kilometre, where the forecasts of Verhulst showed 224. The difference can be explained by the astonishing rise of industry in Belgium, and by the acquisition of the Congo which secured for the country sufficient additional wealth to support the extra population.

The present population of France, exclusive of foreigners, is in remarkable agreement with Verhulst's forecast. The theoretical maximum is almost reached, which explains the low birth-rate and other social phenomena which perturb public opinion. This state of affairs is only a temporary disturbance which will quickly pass with the growing value of the colonies . and the decentralization of the metropolis. It is enough, further, to compare the rapid growth of the French population of Canada with the very slow growth of population in France to understand the biological and economic nature of these phenomena.

Let us return to the population of the United States and compare the concentration in the New World (20 persons per square kilometre) with that already reached in Belgium (266 persons per square kilometre). These figures show that in America the economic and

psychological factors characteristic of the early days of cultivation still predominate, while in Belgium every corner of soil is utilized. It is to this state of things and to this spirit that the co-efficients

$$\varepsilon = \cdot 03134, \quad \omega = 197{,}273{,}000, \quad h = 1 \cdot 6 \times 10^{-10}$$

correspond in equation (8).

A time will come when the more complete utilization of the soil will be as inevitable in America as in Europe, and then the modified vital co-efficients will give an extension of the population curve incompatible with the arc of 1790 to 1930 determined by equation (8).

It should be noted that nothing is as deceptive as the beautiful agreement between the observed and calculated values. A series of observed values is, in fact, equivalent to a narrow band rather than to a curve, and in this band can be traced a number of curves, corresponding very well with the conditions of the problem within the period of the observations, but showing real divergence beyond these limits.

Growth of a Bacterial Colony. After this sociological example a biological one taken from Lotka may be given. It deals with the growth of a colony of bacteria (*B. dendroides*) observed by G. Thornton. In this example we have:

Age, Days		0	1	2	3	4	5
Area occupied in sq. cms.	observed	·24	2·78	13·53	36·30	47·50	49·40
	calculated	·25	2·03	13·08	37·05	47·39	49·02

The calculated values were obtained from the formula

$$p = \frac{\cdot 2524}{e^{-2 \cdot 128t} + \cdot 005125}$$

It is seen that the agreement is as close as possible.

Bacillus coli. Régnier has investigated a number of cultures of *Bacillus coli* varying at the original inoculation from 500 to 500,000 bacteria per c.c. In these experiments the medium was not renewed and the toxic action of accumulating metabolic products ultimately modified the growth-curve, but its beginning agreed closely in all experiments with the Malthusian law (4), with $\varepsilon = 1\cdot12$, whatever might be the original number of germs. We shall return to these experiments in discussing the toxic action of the products of metabolism.

3. Experimental Verification of the Logistic Law

The example of the United States population shows a remarkable agreement between the observations and the logistic law. This agreement is not, however, sufficient, for it is always possible to express a series of numbers that increase and asymptotically approach a limit by a curve having the same properties. The logistic equation may be replaced by another more general equation—

$$p' = F(p) = \phi(p) - \psi(p) \tag{9}$$

where $\phi(p)$ is the increase of population, strictly speaking, and $\psi(p)$ is the total of limiting factors. It is admitted that the action of these factors is scarcely perceptible at the beginning of the process, and that when p is sufficiently great the order of growth of $\psi(p)$ is higher than that of $\phi(p)$. We then have the following inequalities:

$$\phi(p) > \psi(p) \qquad (0 < p < \omega)$$
$$\phi(p) < \psi(p) \qquad (\omega < p)$$

and therefore

$$p'(\omega) = \phi(\omega) - \psi(\omega) = F(\omega) = 0$$
$$F'(\omega) = \phi'(\omega) - \psi'(\omega) < 0.$$

Let $F(p)$ be expanded by Taylor's theorem to the neighbourhood of the point ω. If $(\omega - p)$ is small we get

$$F(p) \sim - (\omega - p)F'(\omega)$$
$$p' = - (\omega - p)F'(\omega)$$

and therefore

$$p \simeq \omega - A e^{F'(\omega)t} \qquad (10)$$

In the same conditions the logistic equation gives

$$p \simeq \omega - \frac{(\omega - p_0)\omega}{p_0} e^{-\alpha t} \qquad (11)$$

Suppose, on the other hand, that $\phi(p)$ is expanded in the same way and p is very small

$$\phi \simeq \phi_0' p + \ldots$$

where $\phi_0 = 0$ and $\phi_0' > 0$ and $\psi(p)$ disappears when $p = 0$. In these conditions, when p is small, equation (9) becomes

$$p' = \phi_0' p$$

and we again get the Malthusian law

$$p = p_0 e^{\phi_0' t}. \qquad (12)$$

Thus in these broad hypotheses on the otherwise arbitrary functions ϕ and ψ, the initial and final parts of the growth of a population follow exponential laws. Junction between these phases is very easy, and in consequence the S-form of the logistic curve may belong to a number of theoretical curves, all satisfying equation (9).

Admittedly, in the case of the logistic law the two exponents are identical:

$$\phi'(0) = - F'(\omega),$$

but this criterion is not certain, for the calculation of exponents is often difficult.

Suppose now that by some means we succeed in modifying the co-efficient of increase, for example, by regularly removing a part of the population proportional to p. Equation (9) becomes

$$p' = \phi(p) - mp - \psi(p)$$

This complementary mortality modifies ω, but it is not possible to say in what direction, for when the functions ϕ and ψ are unknown, the solution Π of the equation

$$\phi(p) - mp - \psi(p) = 0$$

is not related to that of the equation

$$\phi(p) - \psi(p) = 0$$

by any simple expression. On the contrary, in the case of the logistic equation we have

$$p' = (\varepsilon - m)p - hp^2$$

and the modified maximum of the population becomes

$$\Pi = \frac{\varepsilon - m}{h} = \frac{\varepsilon - m}{\varepsilon}\,\omega \qquad (13)$$

In consequence if at the end of this experiment the new maximum Π is found to be connected with the former maximum ω by expression (13), there is a very cogent argument in favour of the logistic law.

This argument occurs in the numerical results of the experiments of Gause on cultures of Paramecium.

E

By taking special precautionary measures to eliminate metabolic products, and by regularly renewing the medium and the food supply, Gause obtained populations which reached the stationary state and maintained it for a relatively long time. For the purpose of numerical control Gause made periodic abstractions of the populated medium. In three series of experiments the fraction removed was $\cdot 1$, $\cdot 2$, and $\cdot 3$ of the medium and hence of the population. If the logistic law is exact, the maxima in these series should be equal to

$$\Pi_1 h = \varepsilon - \cdot 1; \ \ \Pi_2 h = \varepsilon - \cdot 2; \ \ \Pi_3 h = \varepsilon - \cdot 3. \quad (14)$$

Eliminating h and ε from these three equations we get the following relation between the three maxima

$$2\Pi_2 = \Pi_1 + \Pi_3. \quad (15)$$

In the numerical results obtained by Gause there are the following average values:

	Π_1	Π_2	Π_3
Paramecium aurelia . .	475	375	305
Paramecium bursaria .	340	240	190

which closely verify equation (15). This confirmation of the logistic law is much more significant than the close agreement between the theoretical curve (2) and the empirical curve (8). The limiting term in equation (2) is as well represented as the term of multiplication εp.

CHAPTER V

POPULATION AND ENVIRONMENT

In this chapter the growth of a population will be studied while very varied factors will be taken into account: food, available area, immigration, emigration, epidemics, complexity, residual actions, etc.

1. Non-isolated Population

Consider the equation

$$p'(t) = \varepsilon p(t) - h p'(t) + I - E \qquad (1)$$

Several causes can be foreseen that attract or repel immigrants. So far as human population is concerned, there are classes of immigrants who are attracted by the rise of a country; there are on the contrary others whose wish to expatriate themselves increases with the growth of the population and who seek a virgin land. In an animal population, great migrations are almost always provoked by lack of food. Predators especially are mobile and seek the places where food is abundant. These two streams may alternate, and create local fluctuations that may be periodic or periodomorphic.

Express the total of these two streams by a polynomial

$$I - E = v_0 + v_1 p + v_2 p^2 \qquad (2)$$

in which the co-efficients v_0, v_1, and v_2 are positive or negative constants. Equation (1) then becomes

$$p' = v_0 + (\varepsilon + v_1)p - (h - v_2)p^2 \qquad (3)$$

The terms of which expression (2) is composed have not been invented *ad hoc*. The term v_0 expresses the constant fraction of the stream across the frontier, the term $v_1 p$ the positive or negative attraction of a population or the regular withdrawals from bacterial cultures. The term $v_2 p^2$ refers to sudden migrations of predators, etc. A few special cases will be considered.

Unfavourable Case. It may happen that

$$v_0 < 0, \qquad \varepsilon + v_1 < 0, \qquad h - v_2 > 0 ;$$

$p'(t)$ is then always negative and $p(t)$ diminishes and approaches zero.

Favourable Case. Suppose that

$$v_0 > 0, \qquad h - v_2 > 0.$$

The polynomial $v_0 + (\varepsilon + v_1)p - (h - v_2)p^2$ has a negative value with which we are not concerned, and a positive value which may be denoted by ω; then, when $p_0 < \omega$, the derivative $p'(t)$ is always positive, the population $p(t)$ increases and tends towards the limit ω; when $p_0 > \omega$, $p'(t)$ is always negative and $p(t)$ decreases towards the same limit ω.

Unlimited Immigration. Let

$$v_0 > 0, \qquad \varepsilon + v_1 > 0, \qquad h - v_2 < 0 ;$$

in this case the population theoretically increases continually and tends towards infinity. In fact the term $v_2 p^2$ only appears in exceptional circumstances and immigration never lasts long.

Opposing Factors. Suppose that the constant stream v_0 is negative, but the attraction of the neighbourhood is considerable, so that

$$\varepsilon + v_1 > 0 ;$$

in this case two results may appear:

(α) $\qquad (\varepsilon + v_1)^2 + 4v_0(h - v_2) < 0$;

$p'(t)$ is always negative and $p(t)$ tends to zero.

(β) $\qquad (\varepsilon + v_1)^2 + 4v_0(h - v_2) > 0$;

the polynomial $v_0 + (\varepsilon + v_1)p - hp^2$ has two positive limits, ω and $\omega_2 > \omega_1$; when $p_0 < \omega_1$, $p'(t)$ is always negative and $p(t)$ tends to zero; when $\omega_1 < p_0 < \omega_2$, $p'(t)$ is always positive and $p(t)$ increases towards ω_2; when $p_0 > \omega_2$, $p'(t)$ is always negative and $p(t)$ diminishes towards ω_2. Hence in this case the final end of the population depends on the original value p_0, while the two ultimate limiting values o and ω_2 do not depend on p_0. As for ω_2, it is an unstable stationary state.

We shall not consider other possibilities which do not differ essentially from the four cases studied.

2. Periodic Fluctuations of a Homogeneous Population

A homogeneous population under the influence of intermittent factors may pass through periodic fluctuations which the classical form of the logistic equation does not provide for. A population that has reached a certain density may become the victim of an epidemic which only stops when the density has fallen to a limit which renders the propagation of the epidemic impossible. Other causes may produce the same effect, for instance, alternation of the attraction of great cities with a return to the country.

We shall consider the evolution of a population of this kind, assuming that it is originally governed by the logistic law

$$p' = \varepsilon p - hp^2 \qquad (4)$$

and that the epidemic appears as soon as p reaches a certain value Q

$$Q < \omega = \frac{\varepsilon}{h}.$$

At this stage the vital co-efficients become

$$E < \varepsilon, \qquad H > h$$

and equation (4) is replaced by

$$p' = Ep - Hp^2. \tag{5}$$

Suppose that $Q > \dfrac{E}{H}$. The population decreases. A point is reached when the density falls below a certain limit which puts an end to the spread of the epidemic. Let q be the corresponding value of p:

$$q > \frac{E}{H}.$$

At this moment the epidemic ceases, and the population again begins to grow, again following equation (4) until the incidence of a fresh epidemic. In this way there are periodic oscillations of p between q and Q. The period Ω of these oscillations may be calculated. In the first part of the cycle, where $p_0 = q$, we get, using formula 6, from Chapter IV:

$$t - t_0 = \frac{1}{\varepsilon} \log \frac{p(\varepsilon - hq)}{q(\varepsilon - hp)}.$$

Hence the time taken by the first part of the cycle is

$$T_1 = t_1 - t_0 = \frac{1}{\varepsilon} \log \frac{Q(\varepsilon - hq)}{q(\varepsilon - hQ)}. \tag{6}$$

Similarly we get for the second part of the cycle, E being positive,

$$t - t_1 = \frac{1}{E} \log \frac{p(QH - E)}{Q(Hp - E)},$$

which gives for the final point

$$T_2 = t_2 - t_1 = \frac{1}{E} \log \frac{q(QH - E)}{Q(Hq - E)}, \tag{7}$$

and the whole period is equal to

$$\Omega = \frac{1}{\varepsilon} \log \frac{Q(\varepsilon - hq)}{(\varepsilon - hQ)q} + \frac{1}{E} \log \frac{q(HQ - E)}{Q(Hq - E)}. \tag{8}$$

This representation of a two-phased biological process is of course not strictly accurate and needs some revision, but it presents a reasonably correct picture of the mechanism of the formation of *periods of relaxation*. This type of periodicity is often, though incorrectly, contrasted with classical oscillations, for example with elastic oscillations. The latter are, in fact, only a special case of the former. Oscillations of relaxation are much more frequent in nature than classical oscillations and to them must be largely attributed the maintenance of order and the regulation of states of chaos.

The sudden appearance of hordes of small rodents and their no less rapid disappearance may be explained in this way. This phenomenon shows an irregular periodicity with a period in some cases of 9 to 11 years, in others of 3·5 to 4 years. Some authors attribute this periodicity to the action of sunspots, but there is no need for this, for purely terrestrial and even local factors are sufficient to explain it. Consider these factors. First, the observations of Kalabuchow, Sewertzoff,

etc., have demonstrated the importance of the density of an animal population in the appearance, spreading, and disappearance of plagues. Further, a local increase of density attracts predators in large numbers. These two factors will in two or three weeks succeed in destroying 97–98 per cent. of a population of small rodents, and the density falls to the level at which the disease cannot spread. The population, reduced to 2 per cent. of its maximum, finds it refuges sufficient and its food abundant; the new conditions favour a slow increase in numbers, which in a few years re-establishes a state of affairs favourable to another wave of disease. Of course these conditions are never exactly reproduced and the fluctuations are not periodic but periodomorphic.

The speed of reproduction in mice is so great that in the first part of the cycle limiting factors may be neglected, putting $h = 0$. In the second part of the cycle, on the contrary, E is very small in comparison with H, and may be neglected. In this way formulae 6–8 may be given a simpler form:

$$\left. \begin{array}{l} T_1 = \dfrac{1}{\varepsilon} \log \dfrac{Q}{q} \\[2mm] T_2 = \dfrac{Q - q}{QqH} \\[2mm] \Omega = \dfrac{1}{\varepsilon} \log \dfrac{Q}{q} + \dfrac{Q - q}{QqH} \end{array} \right\} \tag{9}$$

These equations enable us to calculate the vital co-efficients

$$\varepsilon = \dfrac{1}{T_1} \log \dfrac{Q}{q}, \qquad H = \dfrac{Q - q}{QqT_2} \tag{10}$$

when Q, p, T_1, and T_2 are known. In the case of mice

$$T_1 \sim 4 \text{ years}, \qquad \frac{Q}{q} \sim 50, \qquad \log \frac{Q}{q} \sim 4$$

whence $\varepsilon \sim 1$.

This value of ε corresponds very well with the rate of multiplication of mice in natural circumstances.

3. Isolated Population Poisoned by its own Metabolic Products: Residual Action

It often happens that the existing state of a system depends not only on the initial values of the variables, but on its whole history. In plant associations one species often "tills the soil" for another by the accumulation of nitrogen compounds. From the mathematical point of view this fertilization is expressed by complementary integral terms in the biological equations. In an animal population the accumulation of metabolic products may seriously inconvenience the whole population or one or other of its members, and this is expressed by a fall in birth-rate and an increase in mortality. If it be assumed, as Volterra has done, that the total toxic action on birth-rate and death-rate is expressible by an integral term in the logistic equation, we get the following integro-differential equation:

$$p'(t) = \varepsilon p(t) - h p^2(t) - c p(t) \int_0^t K(t - \tau) p(\tau) d\tau. \quad (10)$$

The function of residual action $K(t - \tau)$ is a diminishing one. Generally we may write

$$K(0) = 1.$$

It may happen that at the end of a certain time T the residual action ceases to exert an effect, which gives

$$K(t) = 0 \qquad t > T$$

$$p'(t) = \varepsilon p(t) - h p^2(t) - c p(t) \int_{t-T}^{t} K(t-\tau) p(\tau) d\tau. \quad (11)$$

On the other hand, it may happen that residual action lessens but persists indefinitely, which gives

$$\lim_{t \to a} K(t) = \sigma < 1.$$

Simplification. Equation (10) cannot be integrated in its general form; to simplify it put

$$K(t - \tau) = 1 \tag{12}$$

when it becomes

$$p'(t) = \varepsilon p(t) - h p^2(t) - c p(t) P(t) \tag{13}$$

where $P(t)$ is the integral

$$P(t) = \int_0^t p(\tau) d\tau \tag{14}$$

Hence $p(t) = P'(t) \qquad p'(t) = P''(t)$

and equation (13) becomes

$$P'' = \varepsilon P' - h P'^2 - c P P'. \tag{15}$$

Integration. This equation can be integrated. Multiplying it by e^{hP} we may write

$$\frac{d}{dt}\left[e^{hP} P' \right] = \frac{d}{dt}\left[e^{hP}\left(\frac{\varepsilon}{h} + \frac{c}{h^2} - \frac{c}{h} P \right) \right]$$

which after being integrated gives

$$p_0 - \frac{\varepsilon}{h} - \frac{c}{h^2} = e^{hP}\left[P' + \frac{c}{h} P - \frac{\varepsilon}{h} - \frac{c}{h^2} \right] \tag{16}$$

From this we get the solution of equation (13) in parametric form:

$$p = \left(p_0 - \frac{\varepsilon}{h} - \frac{c}{h^2}\right)e^{-hP} + \frac{\varepsilon}{h} + \frac{c}{h^2} - \frac{c}{h}P = F(P) \quad (17)$$

$$t = \int_0^P \frac{ds}{F(s)} \quad (18)$$

These equations give the population p and the time t as functions of a parameter P.

Discussion of the Solution. The population p cannot be negative. Hence the right-hand side of equation (17) vanishes for a finite value of P which we will call P_∞. This value is reached when $t = \infty$, which implies that *the population disappears at the end of a very long time.*

Moreover, supposing that

$$p_0 < \frac{\varepsilon}{h} = \omega$$

we find that p increases with sufficiently small values of t. *Hence there exists a maximum value for the population which is reached in a finite time.* Let p_m be this maximum and t_m the time. It can easily be shown that

$$p_m = \frac{\varepsilon}{h} - \frac{c}{h^2}\log\frac{c + \varepsilon h - p_0 h^2}{c} < \frac{\varepsilon}{h} \quad (19)$$

$$P_m = \frac{1}{h}\log\frac{c + \varepsilon h - p_0 h^2}{c} \quad (20)$$

Substituting this value for P in equation (18) we get t_m. After having passed this maximum, p tends towards zero. There is always one point of inflexion in the interval (t_m, ∞). In the case where

$$p_0 < \frac{3}{4}\omega + \frac{c}{4h^2} - \frac{1}{4}\sqrt{\omega^2 + 6\omega\frac{c}{h^2} + \frac{c^2}{h^4}}$$

there is still one in the interval $(0, t_m)$. Finally, when $p_0 > \omega$, there is no maximum, $p'(t)$ is always negative and the population tends towards zero.

Hence, in every case the accumulation of metabolic products is fatal to a population.

Approximate Formulae. Expressions (17) and (18) are not in a convenient form, and may therefore be replaced by approximate formulae which are not precisely accurate, but which adequately represent the empirical curves. Suppose that c is small in relation to h. Then, when $t < t_m$ we may calculate p by the logistic formula, replacing ω by p_m. This gives

$$p = \frac{p_0 p_m}{p_0 + (p_m - p_0)e^{-\varepsilon t}} \qquad (t < t_m)$$

when $t > t_m$, equation (18) may be written thus:

$$t - t_m = h^2 \int_{P_m}^{P} \frac{ds}{\varepsilon h + c - chs - ce^{-h(s - P_m)}} \qquad (21)$$

using equation (20). We can replace $e^{-h(s - P_m)}$ by its expansion

$$e^{-h(s - P_m)} = 1 - h(s - P_m) + \frac{h^2}{2}(s - P_m)^2 + \ldots$$

and, moreover,

$$P_m = \frac{\varepsilon - hp_m}{c}.$$

Equation (21) now becomes

$$t - t_m = \frac{2}{c} \int_0^{P - P_m} \frac{ds}{\gamma^2 - s^2} \qquad \text{where } 2p_m = c\gamma^2.$$

On integration we get

$$t - t_m = \frac{1}{c} \log \frac{\gamma + P - P_m}{\gamma - P + P_m},$$

whence

$$P - P_m = \gamma th \frac{c(t - t_m)}{2} \tag{22}$$

$$p = \frac{pm}{ch^2 \dfrac{c(t - t_m)}{2}} \qquad (t > t_m) \tag{23}$$

It may be noted that when $h = 0$ this formula exactly represents the growth of a population p from the first moment.

Régnier's Experimental Populations. These results may be applied to J. Régnier's observations, to which reference was made in the last chapter. He was working with cultures of *Bacillus coli* and *Staphylococcus*, in a nutrient medium that was not renewed. The population grew, passed a maximum and finally disappeared. To explain the decrease and final disappearance there is a choice of three hypotheses: (1) lack of food, (2) lack of space, (3) poisoning of the medium by metabolic products. In different ways these three factors lead to the same result—total disappearance of the population. The third hypothesis seems more probable than the others, and we are here concerned with its verification. Unfortunately the counting of bacteria is an operation involving such gross errors that the results can never be very certain.

The co-efficient for B. coli has already been determined—$\varepsilon = 1.14$: the others must now be found.

The following table gives the results of calculation and experiment.

AGE OF POPULATION IN HOURS	p IN MILLIONS	
	Observed	Calculated
0	·5	·5
2	7·3	4·9
4	39·8	47·3
6	380	417
8	802	2126
24	2178	3980
30	3992	3992
48	3574	3830
96	2650	2354
192	354	367

We get $p_m = 3992$, $t_m = 30$ hours.

Equation (23) gives, when $t = 192$

$$ch\ 81c = \sqrt{\frac{3992}{354}} = 3·36$$

whence

$$c = ·023$$

Equation (19) then gives $h \leqslant ·0003$.

The calculated values of p agree very well with the observed values at the beginning and at the end of the process but not very closely between 8 and 24 hours.

The same thing is found for Staphylococcus:

Age (hours)	0	2	4	6	8	24	30	48	96	192
P. obs. (millions)	·5	6·9	32·4	232	628	3049	5366	4029	2285	290
P. calc. (millions)	·5	4·1	33·2	260	1569	5300	5366	5071	1810	290

The second line gives the average of four experiments carried out in identical conditions. The divergence about the averages is very great. The third line gives results calculated with the following parameters

$$p_m = 5366,\ t_m = 30,\ \varepsilon = 1·05,\ c = ·0265,\ h \leqslant ·0002.$$

In spite of the imperfect nature of these results, some interesting facts may be stated. First, the almost equal values of the co-efficients of intoxication c for the two species shows that a chemical factor is involved
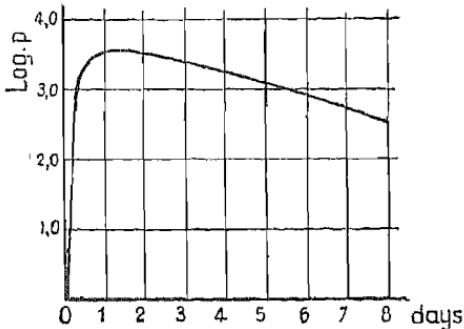
FIG. 8.—BACTERIAL POPULATION
(Staphylococcus)

to which the two species react almost identically. The limiting co-efficients are very small in comparison with the co-efficients of intoxication, c, and h for B. coli is higher than for Staphylococcus. The co-efficients of multiplication ε are almost identical for the two species. Finally for both species the interval 8 to 24 hours gives a great deviation from the logistic law, of the same sign in both cases. This deviation must be ascribed to the effect of the two other factors mentioned.

CHAPTER VI

POPULATION AND ENVIRONMENT
(continued)

DIFFERENTIAL equations of the logistic type or of the more general type (Equation 9, Chap. IV) have one serious defect: the growth of a population is considered without taking into account the sources of food-supply or the area occupied. These factors have a varied and often unexpected action. We shall consider some important cases.

1. One Population Feeding on Another

Imagine a species of animal feeding on plants or on another animal. Let u be the total number or biomass of the predators and v the biomass of the prey in such a population. This problem has already been considered for populations that are not dense. In the more general case the relations between prey and predator can be represented by the system:

$$\left. \begin{array}{l} v' = \varepsilon_1 v - h_{11}v^2 - h_{12}uv \\ u' = - \varepsilon_2 u + h_{21}uv - h_{22}u^2 \end{array} \right\} \tag{1}$$

A full consideration of these equations must be kept for Chapter IX; we are here confined to a few remarks about these equations and their solutions, especially from the point of view of the predators.

First, the form of equations (1) implies a sufficiency of food for the prey, and when this is not so a third

equation must be introduced (see Chapter IX). Secondly, the heterogeneous structure of two populations, as for example in the case of an animal that undergoes metamorphosis, makes considerable caution necessary in drawing conclusions. In some cases it is enough to modify the vital co-efficients; in others it may happen that the mode of feeding is different for larvae and adults, and that a scarcity of food that is fatal to adults may be of no consequence to the larvae. The species has then to be divided into two or more groups.

Two types of solution are possible for equations (1), one of which is favourable to the predators while the other is not. In the first case we have

$$\varepsilon_2 h_{11} < \varepsilon_1 h_{21};$$

an inequality which may be interpreted in several ways. In any case it is favourable to the predators and is of no disadvantage to the prey; the possibility of a final equilibrium results from it. If the limiting co-efficients h_{11} and h_{22} are small enough, the system tends towards a limiting state, passing through decreasing fluctuations which sometimes bear the appearance of periodicity.

In the second case the alternative inequality

$$\varepsilon_2 h_{11} > \varepsilon_1 h_{21}$$

is satisfied and is wholly unfavourable to the predators; at the limit

$$\lim_{t \to \infty} u = 0 \qquad \lim_{t \to \infty} v = \frac{\varepsilon_1}{h_{11}}$$

A peculiar paradox may be noticed in this case.

F

It may happen that at the beginning the food-supply v_0 is present in such quantity that the inequality

$$u'_0 = u_0(- \varepsilon_2 + h_{21}v_0 - h_{22}u_0) > 0$$

is satisfied; u then begins to increase, passes a maximum and falls to zero. To an observer who sees only the predators without noticing the prey, such a case of a population passing a maximum to total extinction in the limit would be very difficult to interpret.

2. A Population Feeding on Abundant Food

Imagine that the food-supply v is so abundant that the loss of $h_{12}uv$ units in unit time is unappreciable; the first of equations (1) then takes the logistic form

$$v' = v(\varepsilon_1 - h_{11}v) ;$$

whence

$$v(t) = \frac{v_0\omega_1}{v_0 + (\omega_1 - v_0)e^{-\varepsilon_1 t}} \quad \text{where} \quad \omega_1 = \frac{\varepsilon_1}{h_{11}} \qquad (2)$$

If the increase of the species u begins at the moment at which that of v is almost finished, v may be replaced by ω_1 in the second of equations (1) and a logistic equation is again obtained for the predators:

$$u' = u(\mathrm{E}_2 - h_{22}u),$$

where the co-efficient of multiplication E_2 is equal to

$$\mathrm{E}_2 = h_{21}\omega_1 - \varepsilon_2.$$

If E_2 is positive the increase of the predators takes place normally. *This example shows the complicated structure of the co-efficient of multiplication of a species and its dependence on external circumstance.*

If, on the other hand, the increase of v is not

complete expression (2) must be introduced into the second of equations (1). The solution of this equation

$$u = \frac{u_0\left[1 + \dfrac{h_{11}v_0}{\varepsilon_1}(e^{\varepsilon_1 t} - 1)\right]^{\frac{h_{21}}{h_{11}}} e^{-\varepsilon_2 t}}{1 + h_{22}u_0\displaystyle\int_0^t \left[1 + \dfrac{h_{11}v_0}{\varepsilon_1}(e^{\varepsilon_1 s} - 1)\right]^{\frac{h_{21}}{h_{11}}} e^{-\varepsilon_2 s}\,ds} \qquad (3)$$

is more complicated than the logistic law, but when

$$\varepsilon_2 h_{11} < \varepsilon_1 h_{21}$$

it has the same character and u tends to the limit

$$\lim_{t \to \infty} u = \frac{\varepsilon_1 h_{21} - \varepsilon_2 h_{11}}{h_{11}h_{22}}$$

In the opposite case u tends to zero.

3. A POPULATION FEEDING ON A LIMITED DIET NOT RENEWED

In this case, which is very common in nature and in human society, system (1) takes the form

$$\left.\begin{aligned} u' &= u(-\varepsilon_2 + h_{21}v - h_{22}u) \\ v' &= -h_{12}uv \end{aligned}\right\} \qquad (4)$$

These equations can easily be integrated. Put

$$U = \int_0^t u(s)\,ds.$$

The second of equations (4) gives

$$v = v_0 e^{-h_{12}U}$$

when the first can be written as

$$u' = u(-\varepsilon_2 + h_{21}v_0 e^{-h_{12}U} - h_{22}u),$$

or

$$(u' + h_{22}u^2)e^{h_{22}U} + \varepsilon_2 u e^{h_{22}U} = h_{21}v_0 u e^{(h_{22} - h_{12})U},$$

which can be integrated giving

$$u = F(u) = \left[u_0 + \frac{\varepsilon_2}{h_{22}} - \frac{h_{21}v_0}{h_{22} - h_{12}} \right] e^{-h_{21}U}$$

$$+ \frac{h_{21}v_0}{h_{22} - h_{12}} e^{-h_{11}U} - \frac{\varepsilon_2}{h_{22}} \qquad (5)$$

$$t = \int_0^U \frac{sd}{F(s)} \qquad (6)$$

Thus the problem is solved. The expression $F(s)$ is positive when $s = 0$ and negative when $s = \infty$. It therefore vanishes for a value of $s = U_\infty$. This means that the predators finally tend to zero. If at the beginning $u'(0) = 0$, that is to say if

$$h_{21}v_0 > \varepsilon_2 + h_{22}u_0$$

the number of predators increases at first, passes a maximum u_m, and then falls to zero. It is easy to calculate u_m, U_m, and t_m. A very interesting biological application of these formulae will appear later.

4. RELATION BETWEEN DENSITY OF POPULATION AND DENSITY OF FOOD-SUPPLY

In certain cases it is possible to study the relative density of a population in relation to its food-supply. It has several times been suggested that the study of density in relation to area should be replaced by that of density in relation to food, and it is undeniable that the suggestion sometimes gives a satisfactory result. We shall consider a biological example taken from

Gause. This author studied the development of two uniform populations, one of which consisted of *Paramecium caudatum* and the other of *Paramecium aurelia*. These protozoa are fed on bacteria in a saline solution regularly renewed and unfavourable to the multiplication of bacteria. In some experiments the Paramecium only received a half-ration per day. In every case one-tenth of the population was periodically removed for checking purposes. If these circumstances are taken into account, the vital co-efficients are found to have the values shown in the following table.

	ε	h
P. caudatum, ordinary ration	1·29	·0089
P. caudatum, half-ration	1·06	·0155
P. aurelia, ordinary ration	1·28	·0265
P. aurelia, half-ration	1·28	·0480

The co-efficient of multiplication is relatively stable, while the limiting co-efficient is inversely proportional to the daily ration.

To explain this result, suppose that the density $\rho = \dfrac{p}{a}$ of a population p in relation to a food-supply a satisfies the logistic equation

$$\rho' = \rho(\varepsilon - h\rho) \tag{7}$$

where the co-efficients ε and h are constant. When the food supply is maintained at a constant rate as in Gause's experiments, equation (7) becomes

$$p' = p(\varepsilon - \frac{h}{a} p) \tag{8}$$

in perfect agreement with experiment. This result may be taken as yet another argument in favour of the

logistic law as the basis of the mathematical theory of population growth.

It may be noted that there is no need for equation (7) in order to justify equation (8). The mutual pressure between the elements of a population becomes greater as food becomes scarcer. Hence it is quite natural that if a maintains a constant value the limiting co-efficient should be inversely proportional to a, while ε does not vary. If a varies, equation (7) no longer fulfils the conditions of the problem and is inconsistent with equation (1).

5. POPULATION AND AREA: FIRST CASE

The area occupied by a population is one of the most important limiting factors. In the case of experimental populations (Drosophila, Protozoa) the influence of the neighbourhood on birth-rate and mortality quickly makes itself felt. Each individual makes its immediate neighbourhood inconvenient for the others. After its death, until its complete disintegration, it still occupies a certain area, in this way hampering the increase of the survivors, even without taking into consideration its defiling of the medium. Two consequences may follow. In the first, this hampering may persist indefinitely. In the second, a dead individual is definitely disintegrated at the end of a certain time and the space it occupied becomes available once again. These two hypotheses finally lead to very different results.

Let p be the density of a population, s the room occupied per unit of volume by living or dead individuals, α the volume of a live individual and β that of a

dead one. Suppose, first, that the birth-rate is proportional to p and to the room available, $1 - s$; secondly, that the death-rate is proportional to p and s; thirdly, that the action of other limiting factors is not negligible and above all affects the birth-rate; fourthly, that β is constant. These suppositions allow us at once to write the equations:

$$p' = pn(1 - s) - mps - hp^2 \qquad (9)$$

$$s = p\alpha + m\beta \int_0^t p(u)s(u)du. \qquad (10)$$

In equation (9) the term $pn(1 - s)$ corresponds to the birth-rate, the term mps to the death-rate, and the term hp^2 to all the unspecified limiting factors. In equation (10) $p\alpha$ denotes the room occupied by the living and the integral term that occupied by corpses.

Transformation of Equations. Differentiation of equation (10) gives

$$s' = \alpha p' + m\beta ps$$

or, including equation (9)

$$s' = p[\alpha n - s(\alpha n + \alpha m - \beta m) - h\alpha p] \qquad (11)$$

Equations (9) and (11) form an integrable system. Eliminating t from these equations

$$\frac{dp}{ds} = \frac{n - (m + n)s - hp}{\alpha n - h\alpha p - s(\alpha n + \alpha m - \beta m)} \qquad (12)$$

and let z be a new variable defined as the quotient

$$z = \frac{n - hp}{hs} \qquad (13)$$

Then $\qquad \dfrac{dp}{ds} = -z - s\dfrac{dz}{ds}.$

The numerator of equation (12) becomes

$$n - (m + n)s - hp = s(hz - m - n)$$

while the denominator may be written

$$\alpha n - h\alpha p - s(\alpha n + \alpha m - \beta m) = s(\alpha hz - \alpha n - \alpha m + \beta m)$$

Put

$$F(z) = \alpha hz^2 + z(h - \alpha n - \alpha m + \beta m) - (m + n) \quad (14)$$

Equation (12) becomes integrable

$$\frac{ds}{s} = - \frac{\alpha hz - \alpha n - \alpha m + \beta m}{F(z)} dz \quad (15)$$

Expression (14) disappears for two values of z

$$z_1 < 0 < z_2.$$

The original values of p and s are connected by the evident relation

$$s_0 = \alpha p_0$$

It follows that in every case s and p satisfy the inequalities

$$s - \alpha p \geqslant 0, \qquad s \leqslant 1$$

Integration. Integration of equation (15) gives s as a function of z

$$s = s_0 e^{-\phi(z)} \quad (16)$$

where

$$\phi(z) = \int_{z_0}^{z} \frac{\alpha h\xi - \alpha n - \alpha m + \beta m}{F(\xi)} d\xi \quad (17)$$

We then get

$$p = \frac{n}{h} - zs_0 e^{-\phi(z)} \quad (18)$$

Equations (16) and (18) give the population p and the volume occupied s in the form of a parameter,

taking no account of time. To introduce this term, the equation

$$\frac{dz}{dt} = - p(z)F(z)$$

must be integrated, which gives the time t as a function of the same parameter z

$$t = \int_z^{z_0} \frac{du}{F(u)\left[\dfrac{n}{h} - us_0 e^{-\phi(u)}\right]} \qquad (19)$$

Equations (16), (18), and (19) completely solve the problem. Since the polynomial F appears in the denominator in the integral in (17) we must make sure that the critical values z_1 and z_2 do not occur in the interval of integration, that is to say that the expression F always has the same sign and that z varies in the same direction.

Effective Integration. Integrate the following. Put

$$\frac{\alpha h\xi - \alpha n - \alpha m + \beta m}{F(\xi)} \equiv \frac{A_1}{\xi - z_1} + \frac{A_2}{\xi - z_2}$$

and we get the following formulae

$$A_1 = \frac{\alpha h z_1 - \alpha n - \alpha m + \beta m}{2\alpha h z_1 + h - \alpha n - \alpha m + \beta m} = \frac{1 + \alpha z_2}{\alpha(z_2 - z_1)}$$

$$A_2 = \frac{\alpha h z_2 - \alpha n - \alpha m + \beta m}{2\alpha h z_2 + h - \alpha n - \alpha m + \beta m} = \frac{1 + \alpha z_1}{\alpha(z_1 - z_2)}$$

where $\qquad\qquad A_1 + A_2 = 1,$

which shows that A_1 and A_2 are positive, less than 1, and that the sign of the difference $A_2 - A_1$ is the opposite of that of the expression $h + \alpha n + \alpha m - \beta m$.

First Case: $z_0 > z_2$. In this case the expression $F(z)$ is always positive, z is a diminishing function of the time and formulae (16), (18), and (19) become

$$
\left.
\begin{aligned}
s &= s_0 \left(\frac{z_0 - z_1}{z - z_1} \right)^{\Lambda_1} \left(\frac{z_0 - z_2}{z - z_2} \right)^{\Lambda_2} \\[2mm]
p &= \frac{n}{h} - z s_0 \left(\frac{z_0 - z_1}{z - z_1} \right)^{\Lambda_1} \left(\frac{z_0 - z_2}{z - z_2} \right)^{\Lambda_2} \\[2mm]
t &= \int_z^{z_0} \frac{du}{\alpha h (u - z_1)(u - z_2) \left[\dfrac{n}{h} - u s_0 \left(\dfrac{z_0 - z_1}{u - z_1} \right)^{\Lambda_1} \left(\dfrac{z_0 - z_2}{u - z_2} \right)^{\Lambda_2} \right]}
\end{aligned}
\right\} (20)
$$

It is to be seen that the space occupied increases more and more, the population reaches a maximum and then diminishes. Two results are possible. It may be that p disappears for a value of z for which s is less than 1. The third of formulae (20) shows that this occurs in a finite time t_1. What happens afterwards? When the value $s = 1$ is reached s no longer varies and equations (10) and (11) may be replaced by

$$ s = 1, \qquad (t \geqslant t_1) $$

Equation (9) becomes

$$ p' = - mp - hp^2 $$

which gives

$$ p = \frac{m p_1 e^{-m(t-t_1)}}{m + h p_1 - h p_1 e^{-m(t-t_1)}} \tag{21} $$

When $t \to \infty$, p tends towards 0 and hence

$$ \lim_{t \to \infty} p = 0, \qquad \lim_{t \to \infty} s = 1 $$

Second Case: $z_1 < z_0 < z_2$. The expression $F(z)$ is always negative, z is an increasing function of time and integration gives

$$
\left.
\begin{aligned}
s &= s_0 \left(\frac{z_0 - z_1}{z - z_1} \right)^{A_1} \left(\frac{z_2 - z_0}{z_2 - z} \right)^{A_2} \\
p &= \frac{n}{h} - s_0 z \left(\frac{z_0 - z_1}{z - z_1} \right)^{A_1} \left(\frac{z_2 - z_0}{z_2 - z} \right)^{A_2} \\
t &= \frac{1}{\alpha h} \int_0^z \frac{du}{(z_2 - u)(u - z_1) p(u)}
\end{aligned}
\right\}
\qquad (22)
$$

In this case the density of the population falls; the space occupied may reach a minimum but ultimately increases. The final result is always expressed by the formula

$$
\lim_{t \to \infty} p = 0, \qquad \lim_{t \to \infty} s \leqslant 1 \qquad (23)
$$

Consequently the process always ends in the disappearance of the population.

6. POPULATION AND AREA: SECOND CASE

Another case, very different from the first may now be considered. Suppose that the dead individuals are definitely disintegrated by the end of a certain time and that the space they occupied becomes available once more. To fix our ideas put:

$$
\beta = \alpha e^{a(t - \tau)}
$$

where $t - \tau$ is the time that has passed since the death of the individual. The first three hypotheses of the last section remain unaltered. In these conditions the

variation of p is again expressed by equation (9); equation (10) may be replaced by

$$s = \alpha p + m\alpha \int_0^t p(u)s(u)e^{\sigma(u-t)} \, du, \qquad (24)$$

and equation (11) by

$$s' = -\sigma s + \alpha p(\sigma + n - ns - hp) \qquad (25)$$

The inequalities

$$1 \geqslant s \geqslant \alpha p$$

are always satisfied. The difference between this case and the last consists in the existence of stable stationary state p_o, s_o, satisfying the equations

$$\left.\begin{array}{r} n - (m + n)s - hp = 0 \\ -\sigma s + \alpha p(\sigma + n - ns - hp) = 0 \end{array}\right\} \qquad (26)$$

In the former case the population p finally disappeared at the end of a finite time; here an indefinite existence is possible.

These results hold good when β is expressed as other functions of the time. If $p(t)$ has a lower limit

$$\beta(t) \geqslant B > 0$$

the population p always disappears at the limit. If on the contrary $\beta(t)$ tends towards zero, a limiting state that is stationary and stable becomes possible. These conclusions have been reached on condition that the metabolic products have no toxic action. If such action appears the disappearance of the population always occurs at the end of a longer or shorter time.

CHAPTER VII

FURTHER MATHEMATICAL TREATMENT OF POPULATION-GROWTH

1. Population Composed of Different Age Groups

VITAL co-efficients always depend on age. Infant mortality in man considerably exceeds the average mortality that appears in biological equations. Moreover, in civilized society limiting factors act indirectly on children, through their parents.

With animals that exhibit metamorphosis, as for example, with insects, it is always necessary to consider the larvae as well as the imagos, and the larvae often live in a different kind of environment. It is therefore quite impossible to make use of the logistic equation to represent all these cases. Each separate population must be treated individually with all the influencing factors and all its own peculiarities. A few special cases will be considered.

Insects with Complete Metamorphosis. Imagine as an example a population of insects with complete metamorphosis, the phases of which cannot co-exist. Let $l(t)$ be the number of larvae, $n(t)$ the number of nymphs, $i(t)$ the number of imagos, and $o(t)$ the number of eggs at a time t. Subdivide the complete annual cycle into four periods:

$$\text{larvae} \rightarrow \text{nymphs} \rightarrow \text{imagos} \rightarrow \text{eggs}$$
$$t_0 - t_1 \qquad t_1 - t_2 \qquad t_2 - t_3 \qquad t_3 - t_4$$

Begin with the larvae. Their original number $l(t_0)$

is proportional to the number of eggs laid by the previous generation. The co-efficient of multiplication of the larvae is simply equal to their mortality; the limiting co-efficient may exist in several cases and one may put

$$l' = - m_1 l - h_1 l^2$$

which gives the modified logistic law

$$l(t) = \frac{l(t_0) m_1}{[m_1 + h_1 l(t_0)] e^{m_1(t - t_0)} - l(t_0) h_1};$$

at the instant of the change to the next phase the number of nymphs is

$$n(t_1) = \lambda_1 l(t_1); \tag{1}$$

the co-efficient $\lambda_1 < 1$ expresses the proportion of full-grown larvae transformed into nymphs.

The nymph phase lasts for a time (t_1, t_2) during which the number of nymphs diminishes according to an exponential law,

$$n(t) = n(t_1) e^{- m_2(t - t_1)}.$$

At the end of this phase the number of imagos is equal to

$$i(t_2) = \lambda_2 n(t_2) = \lambda_2 n(t_1) e^{- m_2(t_2 - t_1)}; \tag{2}$$

the co-efficient $\lambda_2 < 1$ expresses the proportion of full-grown nymphs transformed into imagos.

During the imago phase things go on as in the larval phase, that is to say the decrease of population is governed by the modified logistic law

$$i(t) = \frac{i(t_2) m_3}{[m_3 + h_3 i(t_2)] e^{m_3(t - t_2)} - i(t_2) h_3} \tag{3}$$

where m_3 and h_3 are the co-efficient of mortality and the limiting co-efficient belonging to this phase.

Suppose that eggs are laid at about the moment t_3. The population at this time is equal to $i(t_3)$ and the number of eggs laid is proportional to $i(t_3)$.

$$o(t_3) = \lambda_3 i(t_3) \tag{4}$$

The number of eggs diminishes during the time (t_3, t_4) that elapses between laying and hatching according to the exponential law

$$o(t) = o(t_3)e^{-m_3(t-t_3)}$$

which gives at a time t_4 a number of larvae equal to

$$l(t_4) = \lambda_4 o(t_4) = \lambda_4 o(t_3)e^{-m_4(t_4-t_3)} \tag{5}$$

where λ_4 is the proportion of eggs that hatch.

Replacing $o(t_3)$ by (4), $i(t_3)$ by (3), etc., we get the relation between the number of larvae at the beginning of the next cycle and the original number $l(t_0)$.

$$l(t_4) = \frac{\lambda_1\lambda_2\lambda_3\lambda_4 m_1 m_3 l(t_0)e^{-m_1(t_1-t_0)-m_2(t_2-t_1)-m_3(t_3-t_2)-m_4(t_4-t_3)}}{m_1 m_3 + m_3 h_1 l(t_0)\,(1-e^{-m_1(t_1-t_0)})} \\ + h_3 m_1 l(t_0)e^{-m_1(t_1-t_0)-m_2(t_2-t_1)}.\ (1-e^{-m_3(t_3-t_2)}) \tag{6}$$

At the end of a large number of cycles, l tends towards a limit L

$$L = \frac{m_1 m_3 [\lambda_1\lambda_2\lambda_3\lambda_4 e^{-m_1(t_1-t_0)-m_2(t_2-t_1)-m_3(t_3-t_2)-m_4(t_4-t_3)}-1]}{m_3 h_1(1-e^{-m_1(t_1-t_0)})} \\ + m_1 h_3 e^{-m_1(t_1-t_0)-m_2(t_2-t_1)}.\ (1-e^{-m_3(t_3-t_2)}) \tag{7}$$

as long as

$$\lambda_1\lambda_2\lambda_3\lambda_4 > e^{m_1(t_1-t_0)+m_2(t_2-t_1)+m_3(t_3-t_2)+m_4(t_4-t_3)} \tag{8}$$

This condition is equivalent to the inequality

$$\varepsilon = n - m > 0$$

which is an essential for the existence of a stationary state other than zero in the case of a logistic population.

The same result will be found for the numbers of the imagos at times

$$t_2, \qquad t_2 + T, \qquad t_2 + 2T, \ldots$$

differing by T, the period of the whole cycle.

If the original value $l(t_0)$ is equal to L, there is a stationary state in the sense that at the end of a cycle

$$l(t_0 + T) = l(t_0) = L.$$

If $l(t_0)$ is less than L, $l(t_0 + nT)$ increases and tends towards L, if $l(t_2)$ is greater than L, $l(t_0 + nT)$ decreases and tends towards L. It may again be remarked that the stationary state here is the periodic one with a period T so that

$$l(t + T) = l(t); \qquad i(t + T) = i(t)$$
$$o(t + T) = o(t); \qquad n(t + T) = n(t).$$

The most complex cases, where a certain amount of superposition is possible, may be treated in the same way.

Case of Co-existent Phases. Suppose that the cycle is not a long one and that the co-existence of phases is possible. In this case the number of nymphs becoming imagos is proportional to the number of larvae, and the number of eggs hatching is proportional to the number of imagos. In this way the equations of the system may be written

$$\left. \begin{array}{l} l'(t) = vi(t) - \mu_1 l(t) - k_1 l(t) - h_{11} l^2(t) \\ i'(t) = -\mu_2 i(t) + k_2 l(t) - h_{22} i^2(t) \end{array} \right\} \qquad (9)$$

assuming, naturally, that the larvae and the nymphs belong to different stations and consequently that the limiting co-efficients h_{12} and h_{21} are zero.

Two cases may be distinguished. In the first the

fertility ν and the co-efficients of metamorphosis $k_1 > k_2$ are large enough to diminish the effect of the two mortalities, so that

$$k_2\nu > k_1\mu_2 + \mu_1\mu_2;$$

equilibrium between the two phases is possible and at the limit

$$\lim_{t \to \infty} l = \mathrm{L}, \qquad \lim_{t \to \infty} i = \mathrm{I}$$

where L and I are the positive solutions of the algebraic equations

$$\nu \mathrm{I} = \mathrm{L}(k_1 + \mu_1 + h_{11}\mathrm{L}); \qquad k_2\mathrm{L} = \mathrm{I}(\mu_2 + h_{22}\mathrm{I}).$$

Passage to the limit occurs without fluctuations.

In the case where

$$k_2\nu < k_1\mu_2 + \mu_1\mu_2$$

the two positive factors mentioned are not sufficient and the population vanishes in the limit.

· 2. ANIMALS WITH SEASONAL REPRODUCTION

From many examples dealing with animals with seasonal reproduction we shall choose S. Sewertzoff's observations on grouse and black game in the National Park of Bashkiria. These populations are composed of distinctly different age groups, especially after hatching. Sewertzoff devoted attention to the young group in the period following hatching (the Russian summer months of June, July, and August). He showed that the average number of young per nest diminishes according to the exponential law. This decrease is due to many causes, but chiefly to the activity of many predators. Our equations give a

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satisfactory explanation of this result. Let x be the number of young, y the number of nests, proportional to the number of adults, and z the number of predators. It must be assumed that at the period under consideration there are no unhatched eggs, and hence the population x does not increase; it decreases from very diverse causes such as the death of the young and the complete disappearance of nests owing either to the death of the parents, the severity of the weather, or to predators. Each of these factors has its own place in the equations. As far as predators are concerned, they are in no way restricted by the presence of the adult grouse. In these conditions the equations may be written—

$$x' = - (\mu + m)x - (\lambda_1 + \lambda_2)xz - hxy \qquad (10)$$

$$y' = - my - hy^2 - \lambda_2 yz \qquad (11)$$

$$z' = - \theta z - kz^2 \qquad (12)$$

These equations apply only to the peculiar conditions of the summer months. Let $u = \dfrac{x}{y}$ be the average number of young per nest. Equations (10) and (11) give

$$u' = - u(\mu + \lambda_1 z). \qquad (13)$$

Assuming that the decrease of the predators is much slower than that of the young birds, we get an approximate solution of (13)

$$u = u(0)e^{-(\mu + \lambda_1 z)t} \qquad (14)$$

which reaffirms the statement that the average number of young per nest decreases according to the exponential law.

Using this formula a very close agreement is found with Sewertzoff's figures. For

DATE	JUNE 7 21	JULY 1 13 23	AUG. 2 18
Average {observed \ per nest {calculated	5·7 6 \ 6·2 5·4	5 4 3·9 \ 4·9 4·3 3·9	3·9 2·9 \ 3·6 3·0

and for

DATE	19 JUNE	2 AUG.	17 AUG.
Average {observed \ per nest {calculated	5·4 \ 5·5	4·6 \ 4·3	3·8 \ 3·9

These examples show that for animals with reproductive seasons the dates on which a count is made must correspond to the natural cycle; one can usefully compare only homogeneous statistical facts, that is to say, those relating to dates separated by a complete number of cycles. These facts must be completed by a study of the movements of the population during a cycle.

3. A GENERALIZATION OF THE LOGISTIC LAW

A generalization of the logistic law has been mentioned above

$$p' = F(p) = \phi(p) - \psi(p)$$

where the function $\phi(p)$ represents all the favourable factors and $\psi(p)$ all the unfavourable ones affecting the growth of a population. We shall consider a particular case which to some extent includes the attempts to improve the logistic law. The law is often criticized

on the grounds that the decrease of fertility and increase of mortality are often more rapid than the logistic law implies. Put therefore

$$\phi = npe^{-\nu p} \qquad \psi = mpe^{\mu p} \qquad (16)$$

which gives

$$p' = p[ne^{-\nu p} - me^{\mu p}] \qquad (17)$$

Two very different cases exist. In the first $n < m$ and whatever the original value of p_0, p' is always negative and p tends towards zero.

In the second case, where $n > m$, the equation

$$ne^{-\nu p} - me^{\mu p} = 0$$

has a root ω.

$$\omega = \frac{1}{\nu + \mu} \log \frac{n}{m} \qquad (18)$$

Suppose $p_0 < \omega$; the solution of equation (17)

$$t - t_0 = \int_{p_0}^{p} \frac{ds}{s(ne^{-\nu s} - me^{\mu s})} \qquad (19)$$

gives the time t expressed as a simple integral. The population p tends towards a limit ω.

Its asymptotic expression when t is large enough

$$p \simeq \omega - Ae^{-\eta t} \qquad (20)$$

with $\qquad \eta = me^{\mu \omega} (\nu + \mu)$

is analogous to the logistic law. Moreover, when p_0 is small, equation (17) may be replaced at the beginning of the process by the Malthusian equation.

$$p' = (n - m)p, \qquad p = p_0 e^{(n - m)t} \qquad (21)$$

The essential peculiarities of the logistic law thus appear again, as we have already shown, save for ease

of calculation. This latter argument might be disregarded if it could be demonstrated that equation (17) represents the true state of affairs better than the logistic law. We have shown that the logistic law is well supported by the facts. Moreover, with formula (17) the difficulties of calculation become insuperable for mixed populations, and in reality homogeneous populations do not exist. Hence it is better to make use of the logistic law.

4. SENESCENCE OF A POPULATION

It is often stated that a population, like an organism, is subject to old age expressed by a slowing down of all vital functions. Introduce into equation (15) a diminishing factor $\sigma(t)$ representing senescence

$$p' = F(p)\sigma(t) \tag{22}$$

This equation is easily reduced to (15) by a change in the independent variable. Put

$$u = \int_{t_0}^{t} \sigma(t)dt \tag{23}$$

We get

$$\frac{dp}{dt} = \frac{dp}{du} \cdot \frac{du}{dt} = \frac{dp}{du}\,\sigma(t)$$

and equation (22) becomes

$$\frac{dp}{du} = F(p). \tag{22'}$$

Another form of the equation of senescence may be

$$p' = F(p) + F_1(p)e^{-\sigma t} \tag{24}$$

Admit that

$$F_0(p) > o,$$

as long as p is less than ω, this value being the smallest root of the equation

$$F_0(p) = 0.$$

Admit further that $F'_0(\omega) < 0$, $F_1(\omega) > 0$ and that the functions F_0 and F_1 may be expanded by Taylor's theorem in the neighbourhood of the point ω. As $t \to \infty$, the population p tends towards ω. Two cases may appear:

(i) $$\lambda = - F'_0(\omega) < \sigma;$$

in which case we have the following asymptotic form of p

$$p \sim \omega - ce^{-\lambda t}.$$

(ii) $$\lambda = - F'_0(\omega) > \sigma;$$

in which case

$$p \sim \omega - \frac{F_1(\omega)}{\sigma - \lambda} e^{-\sigma t}$$

This case does not therefore differ qualitatively from the logistic law. A population obeying law (24) always has a maximum ω which it reaches at the end of a long enough time.

Finally a special case of equation (22) may be considered:

$$p' = \varepsilon p e^{-\sigma t}. \tag{25}$$

The solution is

$$p = p_0 e^{\frac{\varepsilon}{\sigma}(1 - e^{-\sigma t})} \tag{26}$$

which, for $t \to \infty$, tends towards the limit

$$\lim p = p_0 e^{\frac{\varepsilon}{\sigma}}$$

Consequently, introduction of the factor of senescence in this case gives the same result as the limiting term in the logistic equation, but with a very important difference: the final value of p *is here exactly proportional to its original value, while in the logistic case it is quite independent of it.*

This independence appears to be well established by observation. Hence, almost without exception, the introduction of the factor of senescence into the theory of the growth of a population is not justified. On the other hand this factor may be of great value in the theory of the growth of an organism.

5. Dynamic Theory of Population-Growth

The chief feature of all these theories of population-growth is their kinetic nature. We speak everywhere of actions and of effects but nowhere do we introduce the idea of force which is so essential both in physics and astronomy. The analogy has suggested to several writers the idea of constructing a differential equation of population-growth as one writes equations for the movement of a body or a medium. In such equations all the forces acting on the system are balanced up: (1) external forces; (2) internal forces and resistances; (3) inertia which balances all the preceding forces. From the mathematical point of view, this 'balance-sheet' is expressed, in the case of a single variable, by a differential equation of the second order.

$$\frac{d^2p}{dt^2} = E + I - R.$$

E denotes the whole of the external forces, I the internal forces, and R the resistances.

In Quetelet's *Physique sociale* there is a very interesting discussion of this problem: "The theory of population may be reduced to the two following principles, which I regard henceforward as the fundamental principles in the analysis of population-growth and the causes that influence it. Population tends to increase according to geometrical progression. The resistance, or the sum of the obstacles to its growth, varies, other things being equal, as the square of the rapidity with which the population increases. Thus, when a population can increase freely, without hindrance, it grows according to a geometrical progression; if the growth takes place among obstacles of all kinds, which tend to check it and which act in a uniform manner, that is to say, if the state of society is not changed, the population does not grow indefinitely, but tends more and more to become stationary."

Inspired by these ideas of Quetelet, Delevski writes the equation of inertia in the absence of all forces as follows,

$$p'' = \varepsilon p', \tag{29}$$

which evidently corresponds to the Malthusian law

$$p' = p_0 e^{\varepsilon t}.$$

Adding to this terms expressing different positive and negative actions, he writes the differential equation

$$p'' = a - bp + (\varepsilon - a')p' - a''p'^2. \tag{30}$$

In this equation $a - bp$ represents an external force, and the terms $a'p'$, $a''p'^2$ correspond to friction or to resistance of the medium in equations of mechanical movement.

I do not wish to criticize or condemn these attempts.

One knows the opposition encountered by Newton's ideas in the scientific world of the seventeenth and eighteenth centuries. As far as the idea of force is concerned, we return to pre-Newtonian times, and in my opinion it is a wise course to take, but one must not forget all the good this idea has done for two centuries. However, it seems to me that equation (29) may be given a preferable form,

$$p'' = \varepsilon^2 p, \tag{31}$$

that is to say that the inertia of population-growth is proportional to p. Further, the general equation of type (30) should be verified by the logistic law but is not, and above all there is lacking a resistance simultaneously proportional to the population and to the rapidity of its growth. With these corrections the equation may be written

$$p'' = a_{00} + (\varepsilon^2 - a_{10})p - a_{01}p' - a_{11}pp' - a_{02}p'^2. \tag{32}$$

This form is more complete than equation (30), more logical, and, in addition, it is verified by the logistic law for the following special values of the co-efficients

$$a_{00} = 0, \ a_{01} = \varepsilon, \ a_{11} = 2h, \ a_{10} = \varepsilon^2, \ a_{02} = 0.$$

Another advantage of this form is that it can easily be integrated when $a_{00} = 0, a_{10} = \varepsilon^2$.

In this case equation (32) becomes

$$p'' + a_{01}p' + a_{11}pp' + a_{02}p'^2 = 0$$

or

$$(p'' + a_{02}p'^2)e^{a_{01}p} + a_{01}p'e^{a_{01}p} + a_{11}p'pe^{a_{01}p} = 0$$

or again, after integration,

$$p' = \mathrm{H}e^{-a_{01}p} - \frac{a_{01}}{a_{02}} - \frac{a_{11}}{a_{02}}p + \frac{a_{11}}{a_{02}^2} \tag{33}$$

and hence

$$t = \int_{p_0}^{p} \frac{ds}{\mathrm{H}e^{-a_{02}s} + \dfrac{a_{11}}{a_{02}^{2}} - \dfrac{a_{01}}{a_{02}} - \dfrac{a_{11}}{a_{02}}s} \qquad (34)$$

The function p given by this equation is qualitatively analogous to the logistic law but is more supple.

Equation (32) may be completed by integral terms expressing the accumulation of residual resistances.

CHAPTER VIII

RELATIONS BETWEEN SPECIES

1. General Considerations

THE problem of the growth of a mixed population recalls that of the development of a homogeneous one; it differs, however, to a considerable extent because the relations between different species naturally take a more complex form than in the case of a homogeneous population. This disconcerting complexity seems to have evaded all analysis and in particular mathematical analysis. However, in the majority of cases these relations may be represented by differential or integrodifferential equations as simple as those studied in the preceding chapters.

It is not a matter of relations between species on the whole of the earth's surface, but between groups in a station that is more or less isolated, or capable of being isolated by a familiar mental process. In this complicated microcosm there exist supplies of food, shelters of very many kinds, and climatic conditions subject to seasonal variation. This assemblage can often be separated into microcosms of a lower order, with almost no visible connection between them.

The species that occur in a station may be found in a large number of others in similar but not identical circumstances. These changes in conditions are expressed in variation of the vital co-efficients. But the future of a mixed population depends on these co-

efficients, so that the probability of this or that result of the struggle for existence may be estimated. Thus we can to a certain extent foresee *a priori* the future of one or of several species in a set of stations of a certain type.

In addition to the permanent factors we shall consider intermittent factors, the effects of which appear when one or more groups exceed a maximum or fall below a certain level, as we saw in the case of small rodents subject to epidemics.

In all these problems two opposed tendencies may appear:

1. The group of organisms occupying a station may tend towards a state of equilibrium.

2. Equilibrium may be impossible.

In the first case a final stable state is reached in practice at the end of a longer or shorter time and is maintained thereafter. This state is independent of the initial state when equations 25 of Chapter II permit only a single set of solutions in the positive region of biological space; in other cases the system tends towards one of the states of stable equilibrium that depend indirectly on the initial state: finally there are certain cases where the final state depends directly on the initial state.

The stability of a biological state is not permanent. The vital co-efficients vary because of imperfect isolation, the appearance of mutations, the intervention of a new factor, and other causes. In human society technical development, improvements in the circumstances of life, a sudden or a continuous variation of the social organization, all have a repercussion on the vital co-efficients.

In the case of instability of a biological system separate mention should be made of the more or less periodic oscillations about a mean state that is neither reached nor approached. It may happen that these oscillations, like Lissajous' figures, may entirely fill a region or an enclosed area in biological space. This dynamic equilibrium has no secular stability.

It is to be observed that the relations between species are not limited to competition and that besides the struggle for existence there is co-operation in many different ways—unilateral (parasitism), or bilateral (symbiosis), sometimes loose or fortuitous, sometimes inseparable. This phenomenon is of great importance, for upon it depend problems of relationship among multicellular organisms.

The vital co-efficients are extremely unstable and the following example gives some idea of their variation. According to Kalabuchow, small rodents like mice, which in nature follow a plainly seasonal cycle, are quite capable in better circumstances of reproduction at all times of the year. A little calculation enables us to evaluate the variation in the co-efficient of multiplication ε. In natural circumstances this co-efficient is of the order of one per annum. Seasonal reproduction gives an annual birth-rate of about twenty per annum, while optimum reproduction gives $n \sim 200$ per annum. This means that in optimum conditions ε is of the order of 180 per annum. Consequently it is quite impossible to look upon the vital co-efficients as an unalterable characteristic of the species whatever may be the circumstances of its life.

To understand the construction of the vital co-efficients, consider a relatively simple case. Suppose that

it is concerned with two species in perpetual struggle for food, and each eating the other on chance encounters. Let p_1 and p_2 be their respective numbers. It is always possible to make a numerical estimate of the probability of the victory of one or the other adversary, and also that of an undecided or drawn battle. For example, let π_1 be the probability of the victory of one (p_1), π_2 the probability of the victory of the other, (p_2) and π_{12} the probability of an indefinite result. Then evidently

$$\pi_1 + \pi_2 + \pi_{12} = 1.$$

Let hp_1p_2 be the number of encounters in unit time. The direct damage from the struggle may be expressed by the term $- h\pi_2p_1p_2$ introduced into the life-equation of the group p_1 and by an analogous term $- h\pi_1p_1p_2$ into the equation of group p_2. This is not all. Encounters that have no result have an effect on the fertility and mortality of the two groups. Further, the fact that an adversary has been eaten is not without influence on the vital co-efficients. This influence is proportional to the number of eaters and the numbers of the eaten, and also depends on the physiological utilization of the food. If the organisms in the two groups are physiologically similar, the terms $+ k\pi_1p_1p_2$ and $+ k\pi_2p_1p_2$ may respectively be added to the life-equations of the two groups. Finally, the result of neutral encounters is expressed by the terms $- l\pi_{12}p_1p_2$ and $- l\pi_{12}p_1p_2$.

In consequence the differential equations of the two groups assume the form

$$\left.\begin{array}{l} p'_1 = \varepsilon_1 p_1 - h_{11}p_1{}^2 - (h\pi_2 - k\pi_1 + l\pi_{12})p_1p_2 \\ p'_2 = \varepsilon_2 p_2 - (h\pi_1 - k\pi_2 + l\pi_{12})p_1p_2 - h_{22}p_2{}^2 \end{array}\right\} \quad (1)$$

or
$$p_1 = \varepsilon_1 p_1 - h_{11}p_1{}^2 - h_{12}p_1p_2 \left. \right\}$$
$$p'_2 = \varepsilon_2 p_2 - h_{21}p_1p_2 - h_{22}p_2{}^2 \left. \right\} \tag{2}$$

where $h_{12} = h\pi_2 - k\pi_1 + l\pi_{12}$

and $h_{21} = h\pi_1 - k\pi_2 + l\pi_{12}$.

Further the quadratic terms $h_{11}p_1{}^2$ and $h_{22}p_2{}^2$ not only express the reciprocal limiting action of the individuals of the same species, but all the external and internal limiting factors.

Thus this particular and relatively simple case of two predatory species that are physiologically similar gives co-efficients of inter-action h_{12} and h_{21} which are not identical, and are positive or negative according to circumstances. In more complex cases complementary terms corresponding to every activity that occurs in a microcosm find places in the biological equations. According to what has been seen in the preceding chapters all these terms are of the order o, 1, or 2, in relation to the numerical effectives of the groups. Terms of a higher order can, however, be foreseen: we may complete the system of two predatory species by a third group p_3 which feeds solely on the remains of the combats between p_1 and p_2. Then the advantage that it receives from this is proportional to the product of the three effectives $p_1p_2p_3$.

2. WHELKS, MUSSELS, BARNACLES

We shall make a study of an extremely interesting cycle observed by E. Fischer-Piette. It concerns the relations between shell-fish (whelks and mussels) and sessile crustaceans (barnacles) observed during a period

of ten years on the mussel-beds of the Pointe du Décollé. The study of these relations enabled Fischer-Piette to perceive the interactions of the three groups after a disturbance of the faunal equilibrium, which had the result of progressively restoring the first equilibrium state. Moreover, the phenomenon of periodicity in mussel-beds is well known. Thus, Fauvel found that in the neighbourhood of St Vaast-la-Hougue the mussels from the Bay of Isigny from time to time rapidly colonize the neighbourhood of St Vaast and then disappear before the attacks of their enemies, man and particularly starfish. This process is made up of the following phases—

1. Rapid development of the mussels.

2. Starfish arrive from all round and, finding an abundance of food, multiply with astonishing speed.

3. Their voracity and the destructive action of man quickly obtain the upper hand of the mussels.

4. As prey fails the starfish tend in their turn to disappear, leaving the field clear for a fresh invasion of mussels.

5. A new cycle begins.

In the case observed by Fischer-Piette the phenomena are more complicated. Whelks can feed on mussels or on barnacles, but have a marked preference for barnacles and eat mussels only in the absence of other food. This predilection is the more surprising because a diet of mussels seems to be much better for them. We shall show that this preference can create and maintain periodic oscillations; but first we shall rapidly set out Fischer-Piette's results.

1. The cycle begins by the reproduction of the barnacles, which cover the rocks with a dense popula-

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tion. This provides food for whelks, which ignore the barnacles below a certain size. The whelks eat barnacles fixed to mussels, not the mussels themselves.

2. The arrival of an abundant hatching of mussels causes the death of the barnacles over a wide area where the latter are swamped by the mussels.

3. The whelks which had previously eaten these barnacles are now deprived of them. They change their diet and begin to pierce the mussels. They multiply enormously; although they only adopt their new diet under pressure of absolute necessity it is much better for them. This increase of whelks results in the rapid diminishing of the mussel bed.

4. When the time comes for the barnacle larvae to settle, surfaces freed from mussels by the activities of the whelks are covered afresh with barnacles.

5. As soon as these barnacles have grown big enough, the whelks return to their original diet and start to eat them. The mussels, left alone by the whelks, are henceforward safe from destruction. The cycle begins again.

Thus, if the mussels happen to increase abnormally, and so have disturbed the equilibrium, one direct consequence of this disturbance (the suppression of the barnacles) is to let loose an antagonistic factor—the whelks begin to destroy them. This destruction will go as far as complete extermination if it does not bring into play another factor to curb the action of the first: the return of the barnacles which attract the whelks from their prey.

Let us now try to express these relations in differential equations. Let p_1 be the number of barnacles, p_2 the number of mussels, and p_3 the number of whelks.

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First Stage. The first stage may be summarized by the following differential equations:

$$\left.\begin{aligned}
p'_1 &= \varepsilon_1 p_1 - h_{13} p_1 p_3 - h_{12} p_1 p_2 - h_{11} p_1^2 \\
p'_2 &= \varepsilon_2 p_2 + h_{21} p_1 p_3 - h_{22} p_2^2 \\
p'_3 &= \varepsilon_3 p_3 + h_{31} p_1 p_3 - h_{33} p_3^2
\end{aligned}\right\} \tag{3}$$

These equations refer to the initial period, characterized by an abundance of barnacles. The absence of the variable p_2 from the third equation implies that the whelks prefer to feed on barnacles (the term $h_3 p_1 p_3$). The term $+ h_{21} p_1 p_2$ in the second of equations (3) shows that the mussels' smothering of the barnacles has begun. Equilibrium is impossible in this phase if the fertility of the barnacles is not great. It is very probable that the inequality

$$\varepsilon_1 < \varepsilon_2 \frac{h_{12}}{h_{22}} + \varepsilon_3 \frac{h_{13}}{h_{33}} \tag{4}$$

is satisfied at this stage. In consequence, population p_1 diminishes, and when it falls below the level $p_1 \leqslant \pi_1$ relations are radically altered.

Second Stage. The barnacle population now exists only sporadically, and the whelks begin to eat the mussels. Then:

$$\left.\begin{aligned}
p'_1 &= \varepsilon_1 p_1 - h_{11} p_1^2 \\
p'_2 &= \varepsilon_2 p_2 - H_{23} p_2 p_3 - H_{22} p_2^2 \\
p'_3 &= E_3 p_3 + H_{32} p_2 p_3 - H_{33} p_3^2
\end{aligned}\right\} \tag{5}$$

During this time the multiplication of the whelks is extremely rapid and it is probable that E_3 satisfies the inequality:

$$E_3 > \varepsilon_2 \frac{H_{33}}{H_{23}}.$$

This implies that equilibrium is impossible during

this stage also and that population p_2 diminishes, liberating rock surfaces for the return of the barnacles, which little by little re-establish themselves. At this point the third stage begins.

Third Stage. The mussels almost disappear and the differential equations assume the form

$$
\left.
\begin{aligned}
p'_1 &= \varepsilon_1 p_1 - \eta_{13} p_1 p_3 - \eta_{11} p_1{}^2 \\
p'_2 &= \varepsilon_2 p_2 - \eta_{22} p_2{}^2 \\
p'_3 &= \varepsilon_3 p_3 + \eta_{31} p_1 p_3 - \eta_{33} p_3{}^2
\end{aligned}
\right\}
\tag{7}
$$

The barnacles are eaten by the whelks, but the second attack of the mussels is only to be seen towards the end of this stage. Thus the relative equilibrium establishing itself during this phase is upset, and the cycle begins again.

Fischer-Piette's memoir gives no figures except for the duration of each phase. From 1925 to 1929 mussels were almost absent: thus the third stage covered four years. In 1929 equilibrium was upset by the arrival of a large hatching of mussels. In 1932 the whelks began to perforate mussels, so that the first stage occupied three years. The shrinking of the mussel-bed has been observed since then.

3. RESIDUAL ACTION

In Chapter V we gave a complete numerical treatment of a special case of residual action; it was concerned with the poisoning of a population by accumulation of its own metabolic products. Other residual actions, accumulating and altering the vital co-efficients, can easily be suggested. For example, theoretically one can foresee the accumulation of hereditary effects

produced by the action of the environment on the organisms, and thus express Lamarck's theory in the form of equations.

We are here limited to the study of reciprocal toxic action between two groups, p_1 and p_2, composing a mixed population. Replace the co-efficients of multiplication by the following equations:

$$\left. \begin{aligned} E_1 &= \varepsilon_1 - c_{11} \int_0^t k_{11}(t-s)p_1(s)ds - c_{12} \\ &\qquad\qquad\qquad \int_0^t k_{12}(t-s)p_2(s)ds \\ E_2 &= \varepsilon_2 - c_{21} \int_0^t k_{21}(t-s)p_1(s)ds - c_{22} \\ &\qquad\qquad\qquad \int_0^t k_{22}(t-s)p_2(s)ds \end{aligned} \right\} \quad (8)$$

The differential equations may be changed into integro-differentials

$$p'_1 = p_1(E_1 - h_{11}p_1 - h_{12}p_2)$$
$$p'_2 = p_2(E_2 - h_{21}p_1 - h_{22}p_2).$$

Common sense insists that a residual action should diminish with time, and the functions of residual action $k_{ih}(u)$ are decreasing functions. Further, the presence of the co-efficients of residual action c_{11}, c_{12}, c_{21}, c_{22}, allows us to write, in general,

$$k_{ih}(o) = 1.$$

The form of these functions can be theoretically deduced from experiments; actually it is not possible to quote any example in which this research leads to a satisfactory result. These functions can then be given the simplest mathematical form. It has been seen that the solution of these integro-differential

equations is a very difficult matter, even in the case of a single variable. Accordingly we here confine ourselves to the study of a few simple examples in which two first approximations are sufficient and these approximations can be satisfactorily calculated. Put throughout

$$k_{11}(u) = k_{12}(u) = k_{21}(u) = k_{22}(u) = 1. \tag{10}$$

Example 1. Imagine a case of two species with zero co-efficients of internal competition, that is to say a mixed population of low density. Equations (9) become:

$$\left. \begin{array}{l} p'_1 = p_1(E_1 - h_{12}p_2) \\ p'_2 = p_2(E_2 - h_{21}p_1) \end{array} \right\} \tag{11}$$

Expand p_1 and p_2 by Taylor's theorem in respect of the parameters $c_{11}, c_{12}, c_{21}, c_{22}, \ldots$

$$\left. \begin{array}{l} p_1 = p_{10} + c_{11}p_{11} + c_{12}p_{12} + c_{21}p_{13} + c_{22}p_{14} + \cdots \\ p_2 = p_{20} + c_{11}p_{21} + c_{12}p_{22} + c_{21}p_{23} + c_{22}p_{24} + \cdots \end{array} \right\} \tag{12}$$

Substituting these expressions in equations (11) gives as a first approximation

$$\left. \begin{array}{l} p'_{10} = p_{10}(\varepsilon_1 - h_{12}p_{20}) \\ p'_{20} = p_{20}(\varepsilon_2 - h_{21}p_{10}) \end{array} \right\} \tag{13}$$

which only differs in notation from equation (18), Chapter II. We then get the following equations for the approximations of the higher orders,

$$\left. \begin{array}{l} q'_1 = \dfrac{q_1 p'_{10}}{p_{10}} - h_{12}p_{10}q_2 - p_{10}A_1 \\[2ex] q'_2 = \dfrac{q_2 p'_{20}}{p_{20}} - h_{21}p_{10}q_1 - p_{20}A_2 \end{array} \right\} \tag{14}$$

where q_1 and q_2 denote a couple of corresponding functions in expansions (12), and A_1 and A_2 are func-

tions depending solely on approximations of a lower order. These equations can be easily integrated. Multiply the first by $\dfrac{p'_{20}}{p_{10}p_{20}}$, the second by $\dfrac{p'_{10}}{p_{10}p_{20}}$, and take the difference of the two results, we get

$$h_{21}q'_1 - h_{12}q'_2 - \varepsilon_2 \frac{d}{dt}\left(\frac{q_1}{p_{10}}\right) + \varepsilon_1 \frac{d}{dt}\left(\frac{q_2}{p_{20}}\right)$$
$$= \frac{A_1 p'_{20}}{p_{20}} - \frac{A_2 p'_{10}}{p_{10}}$$

Integrating this we have

$$q_2 p'_{10} - q_1 p'_{20} = p_{10}p_{20} \int_0^t \left[\frac{A_1 p'_{20}}{p_{20}} - \frac{A_2 p'_{10}}{p_{10}}\right] ds = B(t) \quad (15)$$

in which $B(t)$ denotes the second member. In the first of equations (14) put the function q_2 determined by equation (15), replacing p'_{20} by its value from equation (13) and we get

$$\frac{q'_1 p'_{10} - q_1 p''_{10}}{p'_{10}{}^2} = -\frac{p_{10}A_1}{p'_{10}} - \frac{h_{12}p_{10}}{p'_{10}{}^2}B$$

putting, for simplification,

$$B(t) = p_{10}p_{20}\int_0^t \left[\frac{A_1 p'_{20}}{p_{20}} - \frac{A_2 p'_{10}}{p_{10}}\right]ds.$$

Integrating this equation we get

$$q_1 = -p'_{10}\int_0^t \left[A_1(z) + \frac{h_{12}B(z)}{p'_{10}(z)}\right]\frac{p_{10}(z)}{p'_{10}(z)}\,dz \quad (16)$$

and an analogous expression for q_2

$$q_2 = -p'_{20}\int_0^t \left[A_2(z) - \frac{h_{21}B(z)}{p'_{20}(z)}\right]\frac{p_{20}(z)}{p'_{20}(z)}\,dz \quad (17)$$

These formulae allow us to calculate the second approximations. Put

$$P_{10} = \int_0^t p_{10}(s)\,ds \qquad P_{20} = \int_0^t p_{20}(s)\,ds$$

$$B_{11}(z) = p_{10}(z)p_{20}(z)\int_0^z \frac{P_{10}p'_{10}}{p_{10}}\,ds,$$

$$B_{21}(z) = p_{10}(z)p_{20}(z)\int_0^z \frac{P_{10}p'_{20}}{p_{20}}\,ds.$$

$$B_{12}(z) = p_{10}(z)p_{20}(z)\int_0^z \frac{P_{20}p'_{10}}{p_{10}}\,ds,$$

$$B_{22}(z) = p_{10}(z)p_{20}(z)\int_0^z \frac{P_{20}p'_{20}}{p_{20}}\,ds.$$

We then get the following expressions

$$p_{21} = h_{21}p'_{20}\int_0^t \frac{p_{20}(z)}{p'_{20}{}^2(z)}B_{21}(z)\,dz \qquad p_{11} = \frac{p_{21}p'_{10}}{p'_{20}} - \frac{B_{21}(t)}{p'_{20}} \quad (18)$$

$$p_{22} = h_{21}p'_{20}\int_0^t \frac{p_{20}(z)}{p'_{20}{}^2(z)}B_{22}(z)\,dz \qquad p_{12} = \frac{p_{22}p'_{10}}{p'_{20}} - \frac{B_{22}(t)}{p'_{20}} \quad (19)$$

$$p_{13} = h_{12}p'_{10}\int_0^t \frac{p_{10}(z)}{p'_{10}{}^2(z)}B_{11}(z)\,dz \qquad p_{23} = \frac{p_{13}p'_{20}}{p'_{10}} - \frac{B_{11}(t)}{p'_{10}} \quad (20)$$

$$p_{14} = h_{12}p'_{10}\int_0^t \frac{p_{10}(z)}{p'_{10}{}^2(z)}B_{12}(z)\,dz \qquad p_{24} = \frac{p_{14}p'_{20}}{p'_{10}} - \frac{B_{12}(t)}{p'_{10}} \quad (21)$$

The remaining approximations can be calculated in the same way. Formulae (18) to (21) are not very convenient, but they allow several qualitative conclusions to be drawn in any case of a concrete biological problem in which auto-concurrence can be neglected.

Example 2. Consider another case in which the later approximations follow from the possibility of integration in the first approximation. Let two species be fairly close, so that

$$h_{11}h_{22} - h_{12}h_{21} = 0. \tag{22}$$

Admitting the possibility of expansion (12) we get in the first approximation the equations—

$$\begin{aligned} p'_{10} &= p_{10}(\varepsilon_1 - h_{11}p_{10} - h_{12}p_{20}) \\ p'_{20} &= p_{20}(\varepsilon_2 - h_{21}p_{10} - h_{22}p_{20}) \end{aligned} \Bigg\} \tag{23}$$

We easily get the relation

$$\frac{p_{10}^{h_{21}}}{a_1^{h_{21}}} = \frac{p_{20}^{h_{11}}}{a_2^{h_{11}}} \varepsilon^{(\varepsilon_1 h_{21} - \varepsilon_2 h_{11})t} \tag{24}$$

where a_1 and a_2 denote the initial values of p_1 and p_2.

Let q_1 and q_2 be any pair of corresponding functions in expansion (12); we get

$$\begin{aligned} q'_1 &= \frac{q_1 p'_{10}}{p_{10}} - h_{11}p_{10}q_1 - h_{12}p_{10}q_2 - p_{10}A_1 \\ q'_2 &= \frac{q_2 p'_{20}}{p_{20}} - h_{21}p_{20}q_1 - h_{22}p_{20}q_2 - p_{20}A_2 \end{aligned} \Bigg\} \tag{25}$$

in which the functions A_1 and A_2 only depend on the preceding approximations. From these equations we get

$$h_{21}\frac{d}{dt}\left(\frac{q_1}{p_{10}}\right) - h_{11}\frac{d}{dt}\left(\frac{q_2}{p_{20}}\right) = h_{11}A_2 - h_{21}A,$$

which gives after integration

$$h_{21}\frac{q_1}{p_{10}} - h_{11}\frac{q_2}{p_{20}} = h_{11}\int_0^t A_2 ds - h_{21}\int_0^t A_1 ds \tag{26}$$

This equation, together with (25), enables us to obtain q_1 and q_2 in the following form:

$$\left.\begin{aligned}
q_1 &= p_{10}(t) \int_0^t [p_{20}(z)C(z)h_{22} - A_1(z)]F(t, z)dz \\
q_2 &= - p_{20}(t) \int_0^t [p_{10}(z)C(z)h_{21} + A_2(z)]F(t, z)dz
\end{aligned}\right\} \quad (27)$$

in which

$$C(z) = \frac{h_{11}}{h_{21}} \int_0^z A_2 ds - \int_0^z A_1 ds$$

$$F(t, z) = e^{h_{11}\int_t^z p_{10}ds + h_{22} \int_t^z p_{20}ds}.$$

Apply these formulae to the search for the second approximation. We get

$$\left.\begin{aligned}
p_{21} &= h_{21}p_{20} \int_0^t F(t, z)p_{10}(z)dz \int_0^z P_{10}ds \\
p_{11} &= \frac{p_{10}}{h_{21}} \left[\frac{h_{11}p_{21}}{p_{20}} - h_{21} \int_0^t P_{10}ds\right]
\end{aligned}\right\} \quad (28)$$

$$\left.\begin{aligned}
p_{22} &= h_{21}p_{20} \int_0^t F(t, z)p_{10}(z)dz \int_0^z P_{20}ds \\
p_{12} &= \frac{p_{10}}{h_{21}} \left[\frac{h_{11}p_{22}}{p_{20}} - h_{21} \int_0^t P_{20}ds\right]
\end{aligned}\right\} \quad (29)$$

$$\left.\begin{aligned}
p_{13} &= h_{12}p_{10} \int_0^t F(t, z)p_{20}(z)dz \int_0^z P_{10}ds \\
p_{23} &= \frac{p_{20}}{h_{11}} \left[\frac{h_{21}p_{13}}{p_{10}} - h_{11} \int_0^t P_{10}ds\right]
\end{aligned}\right\} \quad (30)$$

$$p_{14} = h_{12}p_{10} \int_0^t F(t, z)p_{20}(z)dz \int_0^z P_{20}ds \left.\begin{matrix} \\ \\ \\ \\ \end{matrix}\right\}$$

$$p_{24} = \frac{p_{20}}{h_{11}} \left[\frac{h_{21}p_{14}}{p_{10}} - h_{11} \int_0^t P_{20}ds \right] \qquad (31)$$

These formulae show that when h_{11}, h_{12}, h_{21}, h_{22}, ε_1 and ε_2 are positive, the functions p_{11}, p_{12}, p_{23}, p_{24} are always negative and the functions p_{21}, p_{22}, p_{13}, p_{14} always positive. From this we immediately get the following inequalities.

$$p_{21} < \frac{h_{21}p_{20}}{h_{11}} \int_0^t P_{10}ds \qquad p_{22} < \frac{h_{21}p_{20}}{h_{11}} \int_0^t P_{20}ds \left.\begin{matrix} \\ \\ \\ \\ \end{matrix}\right\}$$

$$p_{13} < \frac{h_{11}p_{10}}{h_{21}} \int_0^t P_{10}ds \qquad p_{14} < \frac{h_{11}p_{10}}{h_{21}} \int_0^t P_{20}ds. \qquad (32)$$

These results can be expressed in ordinary language. In the expansion (12) the term p_{10} gives the size of the population p_1 in the absence of toxic actions; the terms $c_{11}p_{11}$ and $c_{12}p_{12}$ express respectively auto-intoxication and intoxication of group p_1 by the metabolic products of group p_2; hence it is natural that these terms are negative. On the other hand, the terms $c_{21}p_{13}$ and $c_{22}p_{14}$ express the advantage which the group derives from the auto-intoxication and intoxication of its neighbours; it is thus natural that these terms should be positive. Similar reasoning applies to group p_2. The inequalities (32) give a rough expression of these advantages and disadvantages. A mixed population of n groups can be treated in the same way.

Mixed Bacterial Populations. As material for experiment there are the figures published by J. Régnier,

and the additional information that he has been good enough to send me, concerning a population composed of *Bacillus coli* and *Staphylococcus*. Régnier's data concerning pure cultures have already been used, and we supplement these results by what can be learnt from mixed cultures. From a qualitative point of view Régnier's figures confirm the theory.

Let p_1 be the number of *B. coli* and p_2 the number of *Staphylococcus* in the mixed culture. Using the values for the vital co-efficients

$$\varepsilon_1 = 1 \cdot 14 \qquad h_{11} = \cdot 0003 \qquad c_{11} = \cdot 023$$
$$\varepsilon_2 = 1 \cdot 05 \qquad h_{12} = \cdot 0002 \qquad c_{22} = \cdot 0265$$

calculated from pure cultures we can calculate the co-efficients of inter-action, $h_{12} \sim \cdot 00005$ and $h_{21} \sim \cdot 00014$, but the distribution about the average is very wide. These values show that in all cases *Staphylococcus* suffers more from living in company than does *B. coli*. The much more rapid decrease in the population p_2 shows that the toxic action of *B. coli* on *Staphylococcus* is greater than the reverse action, but for the moment it is impossible to calculate the co-efficients of residual action with any certainty.

CHAPTER IX

RELATIONS BETWEEN SPECIES (*continued*)

1. TWO SPECIES COMPETING FOR THE SAME FOOD

CONSIDER a population composed of two species p_1 and p_2 in competition for the same, sufficiently abundant, food. Each meeting between the competitors may be followed by a more or less definite struggle or may produce only a mutual inconvenience. Repeating the reasoning of the last chapter, we get the equations:

$$\left. \begin{aligned} p'_1 &= \varepsilon_1 p_1 - h_{11} p_1^2 - h_{12} p_1 p_2 \\ p'_2 &= \varepsilon_2 p_2 - h_{21} p_1 p_2 - h_{22} p_2^2 \end{aligned} \right\} \tag{1}$$

The co-efficients ε_1 and ε_2 are positive, for the two species can very well do without each other. The co-efficients h_{11}, h_{12}, h_{21}, and h_{22} are positive, for it may be supposed that in every case competition between individuals is a net loss to the community.

These equations have been studied by V. Volterra and A. J. Lotka. Volterra assumes that the two competing groups are not widely separated biologically and that the limiting co-efficients are related by the equation

$$h_{11} h_{22} - h_{12} h_{21} = 0 \tag{2}$$

This hypothesis implies that, from the point of view of competition, the two partial populations p_1 and p_2 may be replaced by the imaginary population $\eta_1 p_1 + \eta_2 p_2$.

In these circumstances equations (1) become

$$\left.\begin{array}{l} p'_1 = \varepsilon_1 p_1 - k_1 p_1(\eta_1 p_1 + \eta_2 p_2) \\ p'_2 = \varepsilon_2 p_2 - k_2 p_2(\eta_1 p_1 + \eta_2 p_2) \end{array}\right\} \tag{3}$$

This hypothesis has been discussed in the last chapter. Equations (3) can be integrated:

$$\frac{p_1^{k_2}}{p_2^{k_1}} = \frac{a_1^{k_2}}{a_2^{k_1}} e^{(\varepsilon_1 k_2 - \varepsilon_2 k_1)t} \tag{4}$$

where a_1 and a_2 are the original numbers of the two groups. Two possibilities exist. If

$$\varepsilon_1 k_2 > \varepsilon_2 k_1$$

the first species has a marked advantage over the second, and at the limit

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_1}{k_1 \eta_1}, \qquad \lim_{t \to \infty} p_2 = 0$$

In the alternative

$$\varepsilon_1 k_2 < \varepsilon_2 k_1,$$

$$\lim_{t \to \infty} p_1 = 0, \qquad \lim_{t \to \infty} p_2 = \frac{\varepsilon_2}{k_2 \eta_2}$$

Finally, in the most improbable case in which $\varepsilon_1 k_2 = \varepsilon_2 k_1$, the co-existence of the two groups is possible. Thus, according to Volterra's hypothesis, equilibrium between the two groups is in general impossible, and the smallest disadvantage leads to the disappearance of the corresponding group.

Lotka studied equations (1) in a general way, without imposing condition (2) on the limiting co-efficients. Equations (1) cannot be integrated as easily as equations (3) but it is possible to point out the general

character of their solutions. The following cases may occur.

In the first case, the vital co-efficients satisfy the inequalities

$$\varepsilon_1 h_{22} > \varepsilon_2 h_{12}, \qquad \varepsilon_1 h_{21} < \varepsilon_2 h_{11} \qquad (5)$$

which are equally favourable or unfavourable for the two species; the two groups then tend towards a limiting stable state

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_1 h_{22} - \varepsilon_2 h_{12}}{h_{11} h_{22} - h_{12} h_{21}}, \quad \lim_{t \to \infty} p_2 = \frac{\varepsilon_2 h_{11} - \varepsilon_1 h_{21}}{h_{11} h_{22} - h_{12} h_{21}} \quad (6)$$

In the second case the inequalities

$$\varepsilon_1 h_{22} > \varepsilon_2 h_{12}, \qquad \varepsilon_1 h_{21} > \varepsilon_2 h_{11} \qquad (7)$$

are wholly favourable to the first species, which alone survives:

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_1}{h_{11}}, \qquad \lim_{t \to \infty} p_2 = 0 \qquad (8)$$

In the third case, on the other hand,

$$\varepsilon_1 h_{22} < \varepsilon_2 h_{12}, \qquad \varepsilon_1 h_{21} < \varepsilon_2 h_{11} \qquad (9)$$

the second species is favoured and is the survivor:

$$\lim_{t \to \infty} p_1 = 0, \qquad \lim_{t \to \infty} p_2 = \frac{\varepsilon_2}{h_{22}} \qquad (10)$$

In the fourth case, the inequalities

$$\varepsilon_1 h_{22} < \varepsilon_1 h_{12}, \qquad \varepsilon_1 h_{21} > \varepsilon_2 h_{11} \qquad (11)$$

are the reverse of (5). Here things are more complicated; the process always ends in the disappearance of one of the two competing groups, the other tends towards a limiting stable state determined either by

equations (8) or equations (10). The inclination of the system towards one result or the other depends on the original values of a_1 and a_2. It may be said, broadly speaking, that a much more numerous group alone finally survives.

These results are very interesting from a biological point of view. Equilibrium between two species competing for the same food is possible, but only in a quarter of all the cases which may occur. It follows from equation (5) that in this case we have

$$h_{11}h_{22} > h_{12}h_{21},$$

and hence that the struggle between the two groups is less violent than their internal competition. The contrary would be more probable in the case of two allied species.

We must now apply our remark on vital co-efficients and environment. Two species can live together in a large number of stations in very varied conditions. Vital co-efficients may thus be looked upon as numbers chosen by chance, when the probability of equilibrium between the two groups is only ·25, while that of the disappearance of one of them is ·75. The presence of other groups further decreases the probability of equilibrium. Moreover, the vital co-efficients are not altogether independent, and an increased mortality is almost always accompanied by an increase in the limiting co-efficients. Consequently the chance of co-existence for related groups is very small and in general the influence of natural selection is towards an exaggeration of the differences between the groups. We shall see later that this result remains true for groups in which living hybrids may occur.

2. THREE SPECIES, TWO OF WHICH FEED ON THE THIRD

In the preceding paragraph it has been assumed that the food supply is ample and is independent of the presence of the consumers. If this is not the case, a third equation must be added. Let p_1 and p_2 be the active numbers or biomasses of two predatory species and n the biomass of the prey species. The differential equations take the form:

$$\left.\begin{aligned} p'_1 &= p_1(-\varepsilon_1 + s_1 n - h_{11}p_1 - h_{12}p_2) \\ p'_2 &= p_2(-\varepsilon_2 + s_2 n - h_{21}p_1 - h_{22}p_2) \\ n' &= n(\varepsilon - \sigma_1 p_1 - \sigma_2 p_2 - hn) \end{aligned}\right\} \quad (12)$$

Note that here the co-efficients ε_1, ε_2 are no longer the same as those of equations (11). They represent a negative multiplication of the predators in the absence of their prey.

For brevity the following notation will be used:

$$\left.\begin{aligned} \Delta &= h(h_{11}h_{22} - h_{12}h_{21}) + s_2(h_{11}\sigma_2 - h_{12}\sigma_1) \\ &\quad - s_1(h_{21}\sigma_2 - h_{22}\sigma_1) \\ E_1 &= -\varepsilon_1(hh_{22} + \sigma_2 s_2) + \varepsilon_2(hh_{12} + \sigma_2 s_1) \\ &\quad + \varepsilon(-h_{12}s_2 + h_{22}s_1) \\ E_2 &= \varepsilon_1(hh_{21} + \sigma_1 s_2) - \varepsilon_2(hh_{11} + \sigma_1 s_1) \\ &\quad - \varepsilon(-h_{11}s_2 + h_{21}s_1) \\ E &= -\varepsilon_1(h_{21}\sigma_2 - h_{22}\sigma_1) + \varepsilon_2(h_{11}\sigma_2 - h_{12}\sigma_1) \\ &\quad + \varepsilon(h_{11}h_{22} - h_{21}h_{12}) \end{aligned}\right\} \quad (13)$$

These expressions satisfy the following equations

$$\left.\begin{aligned} E_1(hh_{11} + \sigma_1 s_1) + E_2(hh_{12} + \sigma_2 s_1) &= (\varepsilon s_1 - h\varepsilon_1)\Delta \\ E_1(hh_{21} + \sigma_1 s_2) + E_2(hh_{22} + \sigma_2 s_2) &= (\varepsilon s_2 - h\varepsilon_2)\Delta \\ E_1(h_{11}\varepsilon + \sigma_1 \varepsilon_1) + E_2(h_{12}\varepsilon + \sigma_2 \varepsilon_1) &= (\varepsilon s_1 - h\varepsilon_1)E \\ E_1(h_{21}\varepsilon + \sigma_1 \varepsilon_2) + E_2(h_{22}\varepsilon + \sigma_2 \varepsilon_2) &= (\varepsilon s_2 - h\varepsilon_2)E \end{aligned}\right\} \quad (14)$$

Five cases of stable equilibrium can be distinguished, that is to say, five possible orientations of the system.

First Case. Suppose that

$$\left.\begin{array}{c} E_1 > o, \qquad E_2 > o \\ \varepsilon s_1 - h\varepsilon_1 > o, \ \ \varepsilon s_2 - h\varepsilon_2 > o, \ \ h_{11}h_{22} - h_{12}h_{21} > o \end{array}\right\} (15)$$

and therefore that $\Delta > o$, $E > o$.

These suppositions imply that the situation favours the two predatory species, but that neither of them holds a special advantage over the other. In this case stable equilibrium between the three components is possible and we get the following limiting values:

$$\lim_{t \to \infty} p_1 = \frac{E_1}{\Delta}, \quad \lim_{t \to \infty} p_2 = \frac{E_2}{\Delta}, \quad \lim_{t \to \infty} n = \frac{E}{\Delta} \qquad (16)$$

The limit has been reached without any fluctuation.

Second Case. Suppose on the contrary that the situation favours neither species, that is to say that

$$\varepsilon s_1 - h\varepsilon_1 < o, \qquad \varepsilon s_2 - h\varepsilon_2 < o. \qquad (17)$$

In this case the predators disappear and the prey multiplies to saturation point.

$$\lim_{t \to \infty} p_1 = o, \quad \lim_{t \to \infty} p_2 = o, \quad \lim_{t \to \infty} n = \frac{\varepsilon}{n}. \qquad (18)$$

Third Case. Suppose that

$$\left.\begin{array}{cc} \varepsilon s_1 - \varepsilon_1 h > o, & E_2 < o \\ \varepsilon s_2 - \varepsilon_2 h < o, & E_1 > o \end{array}\right\} \qquad (19)$$

In this case the first species is definitely favoured and finally survives, in equilibrium with the prey, while

I

the second predator disappears; we get, finally, the following limiting values:

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon s_1 - \varepsilon_1 h}{hh_{11} + \sigma_1 s_1}, \quad \lim_{t \to \infty} p_2 = 0, \quad \lim_{t \to \infty} n = \frac{\varepsilon_1 \sigma_1 + \varepsilon h_{11}}{hh_{11} + \sigma_1 s_1} \quad (20)$$

Fourth Case. In this case the second predator is favoured and we have

$$\left. \begin{array}{ll} \varepsilon s_2 - \varepsilon_2 h > 0 & E_1 < 0 \\ \varepsilon s_1 - \varepsilon_1 h < 0 & E_2 > 0 \end{array} \right\} \quad (21)$$

which in the limit gives

$$\lim_{t \to \infty} p_1 = 0, \quad \lim_{t \to \infty} p_2 = \frac{\varepsilon s_2 - \varepsilon_2 h}{hh_{22} + \sigma_2 s_2}, \quad \lim_{t \to \infty} n = \frac{\varepsilon_2 \sigma_2 + \varepsilon h_{22}}{hh_{22} + \sigma_2 s_2} \quad (22)$$

Fifth Case. In this case we have the inequalities:

$$E_1 < 0, \ E_2 < 0, \ \varepsilon s_1 - h \varepsilon_1 > 0, \ \varepsilon s_2 - h \varepsilon_2 > 0 \quad (23)$$

which are partly the reverse of (15). Everything depends on the initial values $p_1(o)$, $p_2(o)$, $n(o)$. The system may move either towards the values of equations (20) or towards those of equations (22).

In comparing these results with those of the preceding paragraph it is seen that variation in the nature of the food effectively lessens the chance of equilibrium between the two species. The equations of the preceding section apply to optimum conditions. Equations (12), on the other hand, take into account the eventual changes in the food-supply. Hence the probability of equilibrium expressed by formula (16) is smaller than that expressed by formula (6) of the earlier section. On the other hand, according to inequalities (17) the probability of extinction of the predators reaches ·25, while it is zero in the earlier section.

3. Two Species, One of which Eats the Other. Volterra's Biological Laws

Consider two species of which the first, p_1, has access to abundant food, which is independent of the presence of the second species, p_2; while the latter is a predator, feeding solely on the species p_1. Differential equations have already been obtained:

$$\left.\begin{array}{l} p'_1 = p_1(\varepsilon_1 - h_{11}p_1 - h_{12}p_2) \\ p'_2 = p_2(-\varepsilon_2 + h_{21}p_1 - h_{22}p_2) \end{array}\right\} \quad (24)$$

expressing the relation between these species. These equations have been considered from the point of view of the predatory species in order to determine the influence of food on the rate of increase of the consumers. Further, in the special case of the absence of quadratic terms, equations (24) express the relation between the animal and vegetable parts of the organic world. These equations will be reconsidered in order to study the influence of rapid variation in the vital co-efficients on the numerical development of the two components.

Suppose, first, that there is no internal competition, either for prey or predator, that is to say that

$$h_{11} = 0, \qquad h_{22} = 0.$$

This is the cyclic case of Volterra

$$\left.\begin{array}{l} p'_1 = p_1(\varepsilon_1 - h_{12}p_2) \\ p'_2 = p_2(-\varepsilon_2 - h_{21}p_1) \end{array}\right\} \quad (25)$$

corresponding to a low density of both populations p_1 and p_2. First write the integral:

$$p_1^{\varepsilon_2} p_2^{\varepsilon_1} e^{-h_{21}p_1 - h_{12}p_2} = H \quad (26)$$

which has been mentioned more than once. Then:

$$h_{21}p'_1 = \varepsilon_1 h_{21}p_1 - h_{12}h_{21}p_1p_2$$

$$h_{12}p'_2 = -\varepsilon_2 h_{12}p_2 + h_{12}h_{21}p_1p_2$$

$$-\varepsilon_2\frac{p'_1}{p_1} = -\varepsilon_1\varepsilon_2 + \varepsilon_2 h_{12}p_2$$

$$-\varepsilon_1\frac{p'_2}{p_2} = \varepsilon_1\varepsilon_2 - \varepsilon_1 h_{21}p_1.$$

Adding these relations we get

$$h_{21}p'_1 + h_{12}p'_2 - \varepsilon_2\frac{p'_1}{p_1} - \varepsilon_1\frac{p'_2}{p_2} = 0$$

the immediate integration of which gives formula (26). H is an integration constant

$$H = a_1{}^{\varepsilon_2}a_2{}^{\varepsilon_1}e^{-h_{21}a_1 - h_{12}a_2} \qquad (27)$$

where $\qquad a_1 = p_1(0), \qquad a_2 = p_2(0).$

In the graph of (p_1, p_2) curves (26) are closed and are without intersections (Fig. 4). Hence the functions $p_1(t)$, $p_2(t)$ are periodic, with a common period ω:

$$p_1(t + \omega) = p_1(t), \qquad p_2(t + \omega) = p_2(t).$$

This periodicity is the subject of the first biological law enunciated by Volterra under the name of the law of the periodic cycle. It has been seen elsewhere that the co-ordinates of the common centre of the closed curves (26) are equal to the averages of the numbers of individuals of the two species during a period of time ω:

$$\overline{p_1} = \frac{1}{\omega}\int_t^{t+\omega} p_1\,dt = \frac{\varepsilon_2}{h_{21}}, \quad \overline{p_2} = \frac{1}{\omega}\int_t^{t+\omega} p_2\,dt = \frac{\varepsilon_1}{h_{12}} \quad (28)$$

This fact is the subject of Volterra's second biological law, the law of conservation of averages.

Having recalled these facts we pass on to Volterra's third biological law. Suppose that for some reason the mortalities of the two species increase. Equations (25) become

$$\begin{rcases} p'_1 = p_1(\varepsilon_1 - \theta_1 - h_{12}p_2) \\ p'_2 = p_2(-\varepsilon_2 - \theta_2 + h_{21}p_1) \end{rcases} \quad (29)$$

in which $\theta_1 < \varepsilon_1$ and θ_2 are the complementary mortalities. Let ω_1 be the corresponding period of these modified equations. Equations (28) assume the form

$$\begin{rcases} \dfrac{1}{\omega_1} \displaystyle\int_t^{t+\omega_1} p_1 dt = \dfrac{\varepsilon_2 + \theta_2}{h_{12}}, \\[2ex] \dfrac{1}{\omega_2} \displaystyle\int_t^{t+\omega_1} p_2 dt = \dfrac{\varepsilon_1 - \theta_1}{h_{21}} \end{rcases} \quad (30)$$

Volterra gives these relations the name of the law of disturbance of averages. It is seen that the complementary mortality of the prey results in a decrease of the average number of predators. Similarly, complementary mortality of the predators results in an increase in the numbers of the prey.

Experimental verification of these laws is extremely difficult because periodic fluctuations corresponding to type (25) have never been observed. In most periodic examples may be seen the periodicity of relaxation, the mechanism of which is very different from that of equation (25) and the laws of Volterra are not applicable to the periodicity of relaxation. Every direct confirmation is therefore extremely valuable. Statistical studies of fish have shown exactly the

indirect repercussion on the prey of an increased mortality of the predators, which confirms Volterra's third law. Gause's experiments on protozoa and on ticks only rarely gave closed curves comparable to (26). In the case of a population composed of *Paramecium bursaria* (predator) and *Saccharomyces exiguus* (prey) it is possible, by artificially thinning the population, to obtain curves resembling the cycles of Volterra. In this way Gause has succeeded in obtaining three consecutive cycles.

One of the causes of the rarity of truly periodic cases is the presence of quadratic terms. Limiting actions expressed by these terms always exist, especially among predators, and it is equation (24) that most accurately expresses the development of the system (p_1, p_2). Two very different cases, which we have already examined, exist. In the first case the inequality

$$\varepsilon_2 h_{11} < \varepsilon_1 h_{21}$$

is equally favourable to both species; for the prey it means that multiplication ε_1 is rapid enough to counteract the destructive power of the predators; for the predatory species it means that the decrease in numbers, ε_2, is relatively small compared with the products of hunting. Thus as a result there is an equilibrium between the two components

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_1 h_{22} + \varepsilon_2 h_{12}}{h_{11} h_{22} + h_{21} h_{12}}, \ \lim_{t \to \infty} p_2 = \frac{\varepsilon_1 h_{21} - \varepsilon_2 h_{11}}{h_{11} h_{22} + h_{21} h_{12}} \quad (31)$$

Finally we get

$$\lim_{t \to \infty} p_1 > \frac{\varepsilon_2}{h_{21}}, \qquad \lim_{t \to \infty} p_2 < \frac{\varepsilon_1}{h_{12}}, \quad (32)$$

that is to say the action of the limiting factors is advantageous to the prey but not to the predators.

When the co-efficients h_{11} and h_{22} are small enough, the functions p_1 and p_2 tend towards the limits of equations (31), passing through decreasing oscillations, exactly analogous to those of mechanical systems with internal resistance. This analogy between limiting factors and internal friction is very interesting. In the language of dynamics which we have used in Chapter VII, the term $-a_{11}pp'$ in equation (32) of that chapter precisely expresses an internal resistance proportional to the population and to the speed of its growth.

On the other hand, when h_{11} and h_{22} are large, the functions p_1 and p_2 tend towards the limits of equation (31) without oscillation.

In the second case we have

$$\varepsilon_2 h_{11} > \varepsilon_1 h_{21}$$

which is unfavourable to the predators, so that they disappear while the first species tends towards saturation point:

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_1}{h_{11}}, \qquad \lim_{t \to \infty} p_2 = 0.$$

These simple results seem not to be in agreement with experiment. The final stable state (31) is but rarely observed. Among the causes of discrepancy may be mentioned the varying age of the prey and the preference of the predators for one or more of the age-groups.

Effect of Age of Prey. Suppose that it is the adults which are chiefly attacked by the predators, while the

young are better protected, either by their smaller size or by their taste or by living in a different station. This case can easily be expressed in equations. Let x_1 be the number of adult prey, x_2 the number of young prey, and p the number of predators. The following equations may be written:

$$\left. \begin{aligned} x'_1 &= -mx_1 + \alpha x_2 - h_{13}x_1 p \\ x'_2 &= nx_1 - (m + \alpha)x_2 \\ p' &= -\varepsilon p + h_{31}p x_1 \end{aligned} \right\} \tag{33}$$

instead of equations (25). The term αx_2 represents the number of young growing into adults, the term nx_1 the birth-rate proportional to the number of adults.

A stable stationary state

$$x_1 = \frac{\varepsilon}{h_{31}}, \ x_2 = \frac{n\varepsilon}{(m+\alpha)h_{31}}, \ p = \frac{\alpha n - m^2 - m\alpha}{h_{13}(m+\alpha)} \tag{34}$$

will establish itself as long as the prey is saved from destruction by its fertility n and by a sufficient survival of its young α, a condition expressible by the inequality

$$\alpha n > m(m + \alpha).$$

On the other hand, if the mortality of the predators is great enough,

$$\varepsilon > \frac{(m+\alpha)\,(\alpha n - m^2 - m\alpha)}{\alpha^2 n^2}$$

the stationary state is a focus, or in other words the system passes through an infinite series of decreasing oscillations, very similar to the cycles of Volterra.

Finally, if the mortality of the prey is too great

$$m(m + \alpha) > \alpha n$$

the two species ultimately disappear.

Hence, equations (33), which here replace equations (25) of the cyclic case, are less favourable to the future of the system and the influence of the varying age of the prey is expressed in a reduction of the chances of survival for either species.

Heterogeneous Predators.   Another cause may complicate the simple cyclic curve or the final equilibrium, and that is complexity in the predatory species.   This species may consist of two forms of different sizes.   If the food p_1 is plentiful the two races co-exist; if food becomes insufficient the dwarf form is favoured.   It requires less food and it is better able to catch the prey in its hiding-places.   The prey being less severely attacked multiplies and so reproduces conditions favourable to the giant form.   This produces oscillations of a very different kind from the fluctuations of Volterra: it is a case that occurred in one of Gause's experiments.   It goes without saying that the two races may differ in other characters.

Didinium nasutum, Paramecium caudatum.   In this experiment of Gause, the population is composed of two species of protozoa, one of which, *Didinium nasutum*, feeds on the other, *Paramecium caudatum*. The ferocity of attack is remarkable and in all Gause's experiments the result was the same: Didinium quickly exterminated Paramecium and then died of starvation. This result is not foreshadowed either by equations (25) or by the more general equations (24).   In this latter case we had two types of equilibrium, neither of which corresponds to reality.   How can this discrepancy be explained?   Return to equations (24).   The terms $h_{12}p_1p_2$ and $h_{21}p_1p_2$ express the interaction between the two species.   As long as the number of encounters is

relatively small, all is well, but if this number becomes large enough the interaction between the species can no longer be thus expressed. A simple example will show the correction to be applied to equations (24). If it is a question of meetings between males and females of the same species, the number of such meetings will be proportional to p^2 and the fertility should be expressed by a quadratic term; now it is in fact expressed by a term of the first order and the number of births in unit time is proportional to the population, not to the square of the population. Hence, if meetings become too frequent, statistical method introduces a term of the first order instead of a quadratic term. Here the extraordinary energy with which Didinium seeks and attacks Paramecium should lead to the same result, and equations (24) should be replaced by

$$\left. \begin{array}{l} p'_1 = \varepsilon_1 p_1 - \mu_1 p_2 - h_{11}{p_1}^2 - h_{12}p_1 p_2 \\ p'_2 = -\varepsilon_2 p_2 + \mu_2 p_2 + h_{21}p_1 p_2 - h_{22}{p_2}^2 \end{array} \right\} \quad (35)$$

as long as the prey exists. In the cyclic case the same correction would give

$$\left. \begin{array}{l} p'_1 = \varepsilon_1 p_1 - \mu_1 p_2 - h_{12}p_1 p_2 \\ p'_2 = -p_2(\varepsilon_2 - \mu_2) + h_{21}p_1 p_2 \end{array} \right\} \quad (36)$$

Consequently, when $\varepsilon_2 > \mu_2$, we get a diminished limit for the prey,

$$\lim_{t \to \infty} p_1 = \frac{\varepsilon_2 - \mu_2}{h_{21}} < \frac{\varepsilon_2}{h_{21}},$$

and the influence of discontinuity in variation would lead to the disappearance of the prey, which the biological equations do not provide for.

Gause has noticed in Didinium a certain dimorphism

leading to unexpected results. If the density of population of the prey falls below a certain limit, difference in size becomes an advantage for the small Didinium. The large predators disappear more quickly than the small ones, and this circumstance may sometimes save small Didinium from destruction. Under experimental conditions, in the absence of proper hiding-places the last Paramecium are quickly exterminated by the last of their small enemies and the whole population finally disappears. This does not occur in nature, where hiding-places are not lacking, and the result may be different. Gause tried to reproduce natural conditions, providing the Paramecium with a refuge inaccessible to the predators, but he did not obtain the expected result because the Paramecium did not leave their refuges and the predators died of starvation. The only way to obtain a relatively stable population was to supplement the two groups at regular intervals by suitably measured additions, and Gause thus obtained the desired result.

To complete these results Gause undertook an interesting statistical experiment. He placed five Paramecium and three Didinium in each of thirty identical tubes. Two days later he found the predators dead in four tubes and in twenty-six tubes a mixed population containing a number of Paramecium varying from two to thirty-eight. In another similar experiment he found, on the sixth day, mixed populations in seventeen tubes out of twenty-five. This result shows that the phenomenon is very complex, and that a distribution that agrees with theory in one of these microcosms cannot be used as evidence in favour of or against any theory whatever.

Bursaria truncatella: Paramecium bursaria.
In another experiment of Gause's, *Bursaria truncatella*
(predator) devoured *Paramecium bursaria* (prey). The
latter were fed on yeast, regularly supplied. Because
of the difference in size, the predators did not succeed

FIG. 9.—RELATIVE GROWTH OF
A MIXED POPULATION
(B. truncatella, P. bursaria) after
Gause.

in exterminating all
the Paramecium and
perished rapidly as soon
as their food began to
fail. Then, in the
absence of predators,
Paramecium multiplied
in the usual way (Fig. 9).

This process is well
suited to mathematical
interpretation, provided
the vital co-efficients
are made to vary in con-
formity with reality,
and the result of discontinuity in biological variation
is observed. Suppose that from the starting-point A
(Fig. 9) to the point B the process is regulated by
equations (24) or (25). From the point B the scarcity
of food becomes appreciable and the few victims that
some of the predators happen to catch are not sufficient
for the whole group : from this moment the co-efficients
h_{21} and h_{12} rapidly diminish, and at about the point C
both co-efficients disappear, or in other words the last
surviving Paramecium are no longer threatened by
predators. From this moment equations (24) or (25)
must be replaced by

$$\frac{dp_1}{dt} = p_1(\varepsilon_1 - h_{11}p_1), \quad \frac{dp_2}{dt} = -p_2(\varepsilon_2 + h_{22}p_2)$$
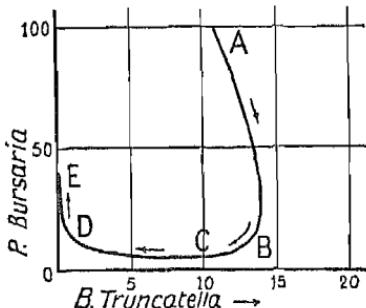
At about the point D there are no more predators. They practically disappear as soon as their numbers fall below a certain limit. The development of Paramecium then continues normally.

Cheyletus eruditus: Aleuroglyphus agilis. Consider further the case of the mites *Cheyletus eruditus* (predator) and *Aleuroglyphus agilis* (prey) studied by Gause and Smaragdova. A new factor appears here, the effect of metabolic products. This factor is the cause of an apparent paradox. Cheyletus placed in a population of its prey of low density can accustom itself to it and even establish a sort of cyclic process. The same mites placed in a dense population of their prey perish rapidly though it would seem that the abundance of food ought to be very favourable. In this case it is again possible to express the phenomenon in equations. According to Gause the smell of the prey is unbearable to its predators. At all events this individual odour of Aleuroglyphus does not prevent a Cheyletus from eating its prey if the surrounding atmosphere is fit to breathe, but robs it of the desire to attack when the personal atmosphere of the prey fills the whole of the space in which they live. It appears that in this case it is not a question of the accumulation of poisonous products but the absence of pockets of respirable air. Let p_1 be the density of the prey, p_2 that of the predators, Π_1, the value of p_1 marking the dividing line between a respirable and irrespirable condition for the predators. The process can be represented by the following equations:

$$\left. \begin{aligned} p'_1 &= p_1(\varepsilon_1 - h_{11}p_1 - h_{12}p_2) \\ p'_2 &= p_2(- \varepsilon_2 + h_{21}p_1 - h_{22}p_2) \end{aligned} \quad (p_1 < \Pi_1) \right\} \quad (37)$$

$$p'_1 = p_1(\varepsilon_1 - h_{11}p_1) \qquad (p_1 > \Pi_1) \\ p'_2 = - E_2 p_2 \qquad \left. \right\} \qquad (38)$$

The co-efficient E_2 represents the increased mortality of the predators in irrespirable air. The value $p_1 = \Pi_1$ cuts the graph (p_1, p_3) into two portions, and the result of the struggle for existence between these species depends on the original numbers of the two populations. Equations (37) and (38) give, broadly speaking, an explanation of Gause and Smaragdova's observations.

It is seen that in many cases Volterra's equations are sufficient to explain the phenomena, but it is not possible to represent a natural process by a single formula which does not take account of sudden or gradual variations in the vital co-efficients.

4. "WOLF—GOAT—CABBAGE"

Populations of several species in chain-like relation, where each link is simultaneously predator and prey, are not uncommon. One case of this kind of population is that of the Island of Komodo in Malaya, inhabited by giant carnivorous reptiles, and by mammals—their food—which themselves feed on the rich vegetation of this island. We may write the differential equations of this biological system, assuming that competition exists only among the plants and that the presence of the reptiles has no direct influence on the vegetation. Let p_1 be the biomass of the mammals, p_2 the number of reptiles, and p_3 the biomass of plants. We get the following equations:

$$p'_1 = p_1(- \varepsilon_1 - h_{12}p_2 + h_{13}p_3) \\ p'_2 = p_2(- \varepsilon_2 + h_{21}p_1) \qquad \left. \right\} \qquad (39) \\ p'_3 = p_3(\varepsilon_3 - h_{31}p_1 - h_{33}p_3)$$

Three different cases exist.

First Case. Suppose that

$$\varepsilon_3 h_{13} h_{21} - \varepsilon_2 h_{13} h_{31} - \varepsilon_1 h_{21} h_{33} > 0 \tag{40}$$

Stable equilibrium is possible with the following limiting values:

$$\left. \begin{array}{l} \lim\limits_{t \to \infty} p_1 = \dfrac{\varepsilon_2}{h_{21}} \\[2ex] \lim\limits_{t \to \infty} p_2 = \dfrac{\varepsilon_3 h_{13} h_{21} - \varepsilon_2 h_{13} h_{31} - \varepsilon_1 h_{21} h_{33}}{h_{12} h_{21} h_{33}} \\[2ex] \lim\limits_{t \to \infty} p_3 = \dfrac{\varepsilon_3 h_{21} - \varepsilon_2 h_{31}}{h_{21} h_{33}} \end{array} \right\} \tag{41}$$

Procedure to the limit may occur either with fluctuations or asymptotically. We do not stress the conditions that make it possible to distinguish the two cases, but note that fluctuations occur when the co-efficient h_{31} is sufficiently small.

Second Case. Suppose that

$$\left. \begin{array}{l} \varepsilon_3 h_{13} h_{21} - \varepsilon_2 h_{13} h_{31} - \varepsilon_1 h_{21} h_{33} < 0 \\[1ex] \varepsilon_3 h_{13} - \varepsilon_1 h_{33} > 0 \end{array} \right\} \tag{42}$$

In this case the food absorbed by plants is sufficient to ensure the existence of a reduced number of mammals, which do not, however, suffice to support the reptiles. Thus we get the following limiting values:

$$\left. \begin{array}{l} \lim\limits_{t \to \infty} p_1 = \dfrac{\varepsilon_3 h_{13} - \varepsilon_1 h_{33}}{h_{13} h_{31}} \\[2ex] \lim\limits_{t \to \infty} p_2 = 0 \\[2ex] \lim\limits_{t \to \infty} p_3 = \dfrac{\varepsilon_1}{h_{13}} \end{array} \right\} \tag{43}$$

or, in other words, the reptiles disappear and the residue, (p_1, p_3) tends towards a stable limiting state.

Third Case. In this case we have

$$\varepsilon_3 h_{13} - \varepsilon_1 h_{33} < 0; \tag{44}$$

the food supplied by plants is not enough to feed the mammals, so that

$$\lim_{t \to \infty} p_1 = 0, \ \lim_{t \to \infty} p_2 = 0, \ \lim_{t \to \infty} p_3 = \frac{\varepsilon_3}{h_{33}}. \tag{45}$$

Thus all animals disappear and the remaining plant population develops alone to its maximum.

What is the probability of these results? To judge from the sign of expression (40), the probability of equilibrium between the three groups is equal to ·5, and that of the two others together is equal to ·5. These figures may explain the relative frequency of three-sided equilibria in nature, but they do not give a reason for the disappearance of these reptiles from all parts save Komodo. This may mean that the estimation of probability in this particular case was not accurate. In fact, in this argument we have implicitly assumed the reciprocal independence of the vital co-efficients, which is not always true. On the other hand, the appearance of new factors is almost always unfavourable to the equilibrium of a system.

SYMBIOSIS AND PARASITISM

1. SYMBIOSIS

THE phenomena of symbiosis and parasitism, interesting and important as they are in themselves, allow us to obtain a better understanding of the mechanism of the evolution of species and the development of organisms. Without sharing the views of several eminent biologists (Famintzine, Merejkovski, Portier) who consider all living matter to be an instance of cellular symbiosis, it is difficult to deny, for example, the symbiotic origin of multicellular organisms. An association of two species, fortuitous at first, may become closer and closer. All possible degrees are known, from a very loose association easily broken to a practically indestructible union in which the partners form an integral whole that cannot be resolved into a mere juxtaposition of two components. This is true of lichens. Admittedly dissociation is still a possibility under laboratory conditions, but these conditions have nothing in common with natural circumstances.

Problems of this kind may be put into the form of equations, not with a view to obtaining numerical results, but in the hope of qualitative conclusions which may have a certain value. Two fundamental types of such equations will be considered.

Groups of Simple Structure. Take first the case of two species of a simple structure, with vital co-efficients almost independent of age. Let x_1, x_2 be the numbers of the free individuals of the two ultimately symbiotic

species, x the number of symbiotic couples, n_1 and n_2 the fertilities in the free state, ν_1 and ν_2 the fertilities in the symbiotic state, m_1 and m_2 the mortalities in the free state and μ_1 and μ_2 the mortalities in the symbiotic state. It may be supposed that a certain number of couples, νx, are born already associated, and that a complementary mortality μ of symbiotic couples must be added to the specific mortalities. Moreover, in certain cases the death of one partner does not involve the death of the other. Besides these factors, which give terms of the first order, meetings between free individuals must be considered, producing $\alpha x_1 x_2$ pairs in unit time. Finally, limiting factors must be considered. In these circumstances, the following differential equations are obtained:

$$\left.\begin{aligned} x'_1 &= \varepsilon_1 x_1 + (\nu_1 - \nu + \beta_1)x - h_{11}x_1{}^2 - h_{13}x_1 x - \alpha x_1 x_2 \\ x'_2 &= \varepsilon_2 x_2 + (\nu_2 - \nu + \beta_2)x - h_{22}x_2{}^2 - h_{23}x_2 x - \alpha x_1 x_2 \\ x' &= (\nu - \mu_1 - \mu_2 - \mu)x - h_{33}x^2 - h_{31}x_1 x - h_{32}x_2 x \\ &\qquad\qquad + \alpha x_1 x_2 \end{aligned}\right\} \quad (\mathrm{I})$$

In these equations each term has an exact biological meaning. The co-efficients are constant but do not possess secular stability and vary with time, sometimes slowly, sometimes rapidly. Before discussion of equations (1) the history of a symbiotic union must be passed in review a history which, in the present case, finds expression in a variation of the vital co-efficients. The story of an association begins with the close approach of two species, originally quite independent of each other.

At the outset, equations (1) have a simpler form:

$$\left.\begin{aligned} x'_1 &= \varepsilon_1 x_1 - h_{11}x_1{}^2 - h_{12}x_1 x_2 \\ x'_2 &= \varepsilon_2 x_2 - h_{21}x_1 x_2 - h_{22}x_2 \end{aligned}\right\} \quad (2)$$

Of course the co-efficients of these equations are different from those of system (1). The two species are never connected and their inter-actions are virtually non-existent :

$$h_{12} \sim 0, \qquad h_{21} \sim 0.$$

In any case, for these co-efficients negative values are more probable than positive values. With this simplification equations (2) become :

$$\begin{aligned}
x'_1 &= \varepsilon_1 x_1 - h_{11} x_1{}^2 \\
x'_2 &= \varepsilon_2 x_2 - h_{22} x_2{}^2
\end{aligned} \tag{3}$$

Suppose that these living objects inhabiting the same environment can fortuitously enter into very loose associations, no more, perhaps, than a mere approach that is advantageous to both. The chances of such meetings are not zero, and any event of which the probability is not zero is bound to occur. Hence by the side of free individuals will appear a certain number of couples, the chance partners in which find an advantage in their association. Equations (3) will become :

$$\left.\begin{aligned}
x'_1 &= \varepsilon_1 x_1 + \beta_1 x - h_{11} x_1{}^2 - h_{13} x_1 x - \alpha x_1 x_2 \\
x'_2 &= \varepsilon_2 x_2 + \beta_2 x - h_{22} x_2{}^2 - h_{23} x_2 x - \alpha x_1 x_2 \\
x' &= -(\mu_1 + \mu_2) x - h_{33} x^2 - h_{31} x x_1 - h_{32} x x_2 + \alpha x_1 x_2
\end{aligned}\right\} \tag{4}$$

The terms $\beta_1 x$ and $\beta_2 x$ correspond to the eventual separation of the couples. The term $\alpha x_1 x_2$ expresses the formation of couples; the limitative co-efficients h_{13}, h_{23}, h_{31}, and h_{32} express the inter-actions between couples and free individuals. The association has advantages, and hence the limitative co-efficients satisfy the following inequalities :

$$\left.\begin{aligned}
h_{33} &< h_{31} < h_{11} < h_{13} \\
h_{33} &< h_{32} < h_{22} < h_{23}
\end{aligned}\right\} \tag{5}$$

In the initial stage (3) there is a state of equilibrium:

$$x_1 = \frac{\varepsilon_1}{h_{11}}, \qquad x_2 = \frac{\varepsilon_2}{h_{22}}.$$

In stage (4) the equilibrium satisfies the following inequalities:

$$x_1 < \frac{\varepsilon_1}{h_{11}}, \quad x_2 < \frac{\varepsilon_2}{h_{22}}, \quad x^2 < \frac{\alpha x_1 x_2}{h_{33}}.$$

This implies that the formation of the third group (the couples) results in a decrease of the two free groups. On the other hand, too great a decrease in the numbers of free individuals is not an advantage to the symbionts. However, since the association is admittedly advantageous, the working of competition and of elimination may lead to the disappearance of free individuals and in consequence to the disappearance of symbiotic pairs. In these circumstances two solutions are possible. First, the symbiotic condition may become hereditary. The formation of a symbiotic pair becomes possible in what may be called the common domain of a couple. Some of the gametes of one of the associated species may already contain the gametes or even the adults of the other. In the case in which this phenomenon is in partial existence the process is regulated by equations (1) which follow chronologically upon the expressions (5). The next stage is the total disappearance of the free groups. System (1) is then reduced to the logistic equation:

$$x' = (\nu - \mu)x - hx^2 \tag{6}$$

This is the case with regard to lichens. The wood-eating Termites which contain symbiotic flagellate Protozoa have not reached this stage, but they have

lost the ability to live independently. Other examples of this kind of evolution might be indicated.

Groups of Heterogeneous Structure. We shall now consider the case of two different species, choosing among many examples the association of *Eupagurus* and *Adamsia*. The larvae of these animals lead a free life in different circumstances from the adults, and develop in different oecological zones. Let x be the number of symbiotic pairs, x_{11} and x_{12} the respective numbers of larvae and adults of Eupagurus, x_{21} and x_{22} the corresponding numbers of Adamsia. It must be supposed that in the free state the larvae are not in competition with the adults and that there is no interaction between the two species.

First Stage. The first stage is expressed by the following equations:

$$\left.\begin{array}{l} x'_{11} = n_1 x_{12} - m_1 x_{11} - k_1 x_{11} - h_1 x_{11}^2 \\ x'_{12} = k_1 x_{11} - \tau_1 x_{12} - g_1 x_{12}^2 \end{array}\right\} \quad (7)$$

$$\left.\begin{array}{l} x'_{21} = n_2 x_{22} - m_2 x_{21} - k_2 x_{21} - h_2 x_{21}^2 \\ x'_{22} = k_2 x_{21} - \tau_2 x_{22} - g_2 x_{22}^2 \end{array}\right\} \quad (8)$$

Equations (7) refer to Pagurus and equations (8) express the development of the Adamsia population before the formation of the symbiotic couples. A state of equilibrium between the two groups, each composed of one species, is theoretically possible but is never realized. Pagurus is a mobile animal, ill-protected against its many dangerous foes. It provides itself with a movable shelter in the shape of the shell of a gasteropod mollusc. Adamsia is an animal unable to move by its own power, feeding on prey brought to it by the current and provided with acontia as a means of defence. By chance encounters, the same shell may

protect the Pagurus and carry the Adamsia. It must be supposed that at this initial stage the acontia are no danger to Pagurus, or otherwise the formation of the association would be impossible. The two partners in the association have an advantage over their free brethren. Their mortalities and their limitative co-efficients are certainly diminished, and equations (7) and (8) by the addition of compensating terms and a fifth equation taking into account the formation of the couples would then assume the form—

$$\left.\begin{aligned}
x'_{11} &= n_1 x_{12} - m_1 x_{11} - k_1 x_{11} - h_1 x_{11}{}^2 + n_1 x \\
x'_{12} &= k_1 x_{11} - \tau x_{12} - g_1 x_{12}{}^2 - h_{13} x_{12} x - \alpha x_{12} x_{22} \\
x'_{21} &= n_2 x_{22} - m_2 x_{21} - k_2 x_{21} - h_2 x_{21}{}^2 + n_2 x \\
x'_{22} &= k_2 x_{21} - \tau_2 x_{22} - g_2 x_{22}{}^2 - h_{23} x_{22} x - \alpha_{12} x_{22} \\
x' &= - (\mu_1 + \mu_2 + \mu) x - h_{33} x^2 - h_{31} x_{12} x \\
&\quad - h_{32} x_{22} x + \alpha x_{12} x_{22}.
\end{aligned}\right\} \tag{9}$$

These equations represent a state of affairs created and maintained by purely fortuitous meetings during the search for shelter by Pagurus and for resting places by Adamsia larvae. There has been no pre-adaptation of the two species to a common life. A few individuals have merely been favoured by chance, and nothing more.

Second Stage. This state might have persisted indefinitely but for the working of selection. In some instances selection eliminates fresh mutations, in others it removes the less favoured ones. The latter eventuality seems to be the more probable. Hence the working of selection increases the fortuitous advantage of the commensal pairs. This process may be illustrated by several examples of Pagurus in more or less close symbiosis with anemones. For example, the case of

Eupagurus prideauxii and *Adamsia palliata* represents the highest point in this evolution. The reciprocal adaptation is very close. Adamsia, very sensitive to external irritation, nevertheless offers no resistance to its capture by a *Eupagurus prideauxii*; it is unable to live if separated from the hermit-crab, and the latter, if deprived of its companion, does all it can to restore the symbiotic condition.

To understand the working of the evolutionary mechanism, look closely at equations (9). Suppose that a state of equilibrium is nearly reached. The values of the variables satisfy the following inequalities:

$$x^2 < \frac{\alpha x_{12} x_{22}}{h_{33}}; \quad \alpha x_{12} x_{22} < k_1 x_{11}; \quad \alpha x_{12} x_{22} < k_2 x_{21}.$$

It follows that each decrease in $x_{12} x_{22}$ results in a decrease in x. The struggle for existence among the hermit-crabs is very keen, and it would seem that any advantage acquired by the symbiotic pairs must result in the total destruction of the species. This is where the second solution, of which we have spoken, comes into consideration. The existence of the larval phase of the two species explains everything. The appearance of mutants with tropisms resulting in mutual attraction increases the co-efficient α and consequently increases the proportion of couples in this mixed population. At the same time, the average age at which association occurs falls in both species. Free adults become rarer, especially adults of mature age, and the terms $n_1 x_{12}$, $n_2 x_{22}$, expressing the number of larvae proceeding from free groups, become negligible in comparison with the terms $n_1 x$, $n_2 x$, which express the numbers of larvae of symbiotic origin. On the other hand, the number of

couples formed in unit time becomes more and more proportional to the product $x_{11}x_{12}$, for young animals, after having emerged from the larval state, either find symbiotic shelter or very rapidly disappear. In this way equations (9) are simplified:

$$\left.\begin{aligned}
x'_{11} &= n_1 x - m_1 x_{11} - k_1 x_{11} - h_1 x_{11}^2 \\
x'_{12} &= k_1 x_{11} - \tau_1 x_{12} - g_1 x_{12}^2 - h_{13} x_{12} x - \alpha x_{11} x_{21} \\
x'_{21} &= n_2 x - m_2 x_{21} - k_2 x_{21} - h_2 x_{21}^2 \\
x'_{22} &= k_2 x_{21} - \tau_2 x_{22} - g_2 x_{22}^2 - h_{23} x_{22} x - \alpha x_{11} x_{21} \\
x' &= -(\mu_1 + \mu_2 + \mu) x - h_{33} x^2 + \alpha x_{11} x_{21}
\end{aligned}\right\} \quad (10)$$

If the co-efficients of fertility n_1, n_2 are large enough, equations (10) lead to a stable limiting state. Among other species of hermit-crab the association with anemones is less intimate than that of *Adamsia palliata* and *Eupagurus prideauxii*. Thus the anemone Sagartia associates with a hermit-crab but is also able to live without it.

2. SIMPLE PARASITISM

Parasitism may, in general, be treated as a special case of symbiosis by modifying the hypotheses concerning the vital co-efficients in such a way as especially to favour one species while maintaining the life of the other. But parasitism profoundly changes organisms and so deserves special study.

Example 1: Entomophagous parasites. Following a series of notes by W. R. Thompson on the action of entomophagous parasites, A. J. Lotka completed that writer's analysis with a system of differential equations of the first order.

Admit, with W. R. Thompson, that two species be found together: the host, a noxious insect, and the

parasite, introduced to destroy the insect. A parasite lays on the host a certain number of eggs of which, on an average, k hatch and produce larvae, which in turn are transformed into free-living adults. Each oviposition of the parasite leads ultimately to the destruction of the infested host. Let p_1 be the number of uninfested hosts and p_2 the number of free adult parasites seeking an insect host on which to deposit their eggs. The development of the two species may be expressed by two equations of the type—

$$\left.\begin{aligned}
p'_1 &= \varepsilon_1 p_1 - h_{11} p_1{}^2 - h_{12} p_1 p_2 \\
p'_2 &= k h_{12} p_1 p_2 - m_2 p_2 - h_{22} p_2{}^2
\end{aligned}\right\} \quad (11)$$

The squared terms represent, as always, the total action of all the limitative factors. The term $k h_{12} p_1 p_2$ expresses the total number of parasite's eggs hatched out in unit time. Equations (11) permit three stationary states.

1. *Destruction of the two species.*

$$p_1 = 0, \qquad p_2 = 0;$$

this state is stable only where ε_1 is negative.

2. *Repulse of the parasites.*

$$p_1 = \frac{\varepsilon}{h_{11}}, \qquad p_2 = 0;$$

this state is stable only when

$$k \varepsilon_1 h_{12} < m_2 h_{11}.$$

3. *Co-existence of the two species.*

$$p_1 = \frac{h_{22} \varepsilon_1 + h_{12} m_2}{h_{11} h_{22} + k h_{12}{}^2}, \quad p_2 = \frac{k h_{12} \varepsilon_1 - m_2 h_{11}}{h_{11} h_{22} + k h_{12}{}^2};$$

this state is stable only when

$$k \varepsilon_1 h_{12} > m_2 h_{11}.$$

We shall discuss these results from the practical point of view. Theoretically, the introduction of parasites is not sufficient for complete destruction of the host. In the most favourable case the system $(p_1 p_2)$ tends towards an equilibrium value which is not zero. However, by choosing a sufficiently large original number of parasites the curve can be made to approach as closely as is wished to the p_2 axis and so to obtain total destruction of the hosts.

In practice it is essential to take into account the interdependence between the numbers of the hosts and the fertility of the parasites. In the experiments of Smirnov and Kusin on *Mormoniella vitripennis*, a parasite on the fly *Calliphora erythrocephala*, a number of flies varying from one to a hundred were put at the disposal of a pair of parasites. Each experiment lasted for an average of twelve days: the results are given in the following table:

NUMBER OF NYMPHS	1	2	3	5	10	25	50	64	98
No. of parasites per nymph .	22·6	23·8	22·4	22·3	18·8	14·1	9·0	10·7	7·8
Total no. of parasites .	22·6	47·5	67·2	111·4	187·5	352·5	451	682	745

Similar results were obtained with the common housefly:

NUMBER OF NYMPHS	1	2	3	5	10	25	50	84	89
No. of parasites per nymph .	12·4	8·8	7·5	7·3	6·4	5·7	5·4	2·5	4
Total no. of parasites .	12·4	17·5	22·6	36·5	64·4	142	268	212	354

It may be asked to what extent this multiple infestation contributes to the destruction of the flies. The

result depends on the host. The proportion of surviving flies, which is very small for *Calliphora*, is considerable for *Musca domestica*. Hence total destruction of flies does not occur and equations (11) of Lotka need serious revision.

In the following examples we shall study the action of parasites on the vital co-efficients and on the fate of their hosts.

Example 2. Consider a case in which parasitism is maintained by the co-existence of healthy and infested hosts. Suppose, first, that multiple infestation does not occur and that the parasite does not multiply within the host; secondly, that infestation is due to free larvae coming from without; thirdly, that the number of parasitic larvae is proportional to the number of infected hosts; fourthly, that the parasites do not influence the vital co-efficients of the hosts; and fifthly, that the hosts are born healthy. This gives very favourable conditions for the hosts.

Let x be the number of free hosts and y the number of infected ones. Write the equations:

$$\left. \begin{array}{l} x' = ny + \varepsilon x - hx^2 - hxy - \alpha xy \\ y' = - my - hxy - hy^2 + \alpha xy \end{array} \right\} \qquad (12)$$

The term αxy expresses the number of healthy hosts infected in a unit of time. Note that the whole population obeys the logistic law:

$$x' + y' = \varepsilon(x + y) - h(x + y)^2. \qquad (13)$$

Two possibilities exist for the distribution of this population between the two groups. In the first

$$\alpha > h, \qquad \frac{m}{\alpha - h} < \frac{\varepsilon}{h}$$

which implies that the production of parasites is large enough to ensure the maintenance of the group of parasitized hosts by the side of the healthy group. Then at the limit:

$$\lim_{t \to \infty} x = \frac{n}{\alpha}, \qquad \lim_{t \to \infty} y = \frac{\varepsilon\alpha - nh}{\alpha h}.$$

In the second case

$$\alpha - h < \frac{hm}{\varepsilon},$$

which implies that the reproduction of the parasites is not sufficient to keep the infected group from extinction. In the limit:

$$\lim_{t \to \infty} x = \frac{\varepsilon}{h}, \qquad \lim_{t \to \infty} y = 0.$$

Hence, in the first case the two groups co-exist, in the second the population rids itself of the parasites.

Example 3 : Parasitic Castration. Suppose that the hypotheses of Example 2 remain valid save that contamination renders the host incapable of reproduction. Equations (12) are then to be replaced by others:

$$\left. \begin{array}{l} x' = \varepsilon x - hx^2 - hxy - \alpha xy \\ y' = -my - hy^2 - hxy + \alpha xy \end{array} \right\} \qquad (14)$$

which differ by the absence of the term ny representing the birth-rate among infected hosts. This hypothesis does not alter the final result: the two possibilities of the preceding paragraph remain. In the first case

$$\alpha\varepsilon - hn > 0,$$

which means that the reproduction of parasites is

sufficient to ensure the maintenance of the infected group by the side of the healthy group. At the limit

$$\lim_{t \to \infty} x = \frac{m}{\alpha} + \frac{hn}{\alpha^2}, \quad \lim_{t \to \infty} y = \frac{\varepsilon\alpha - hn}{x^2}.$$

In the second case

$$\alpha\varepsilon - hn < 0$$

which means that the multiplication of the parasites is insufficient and that the process ends with the total disappearance of contaminated hosts:

$$\lim_{t \to \infty} x = \frac{\varepsilon}{h}, \qquad \lim_{t \to \infty} y = 0.$$

Example 4 : Parasitic Action Increases the Mortality of the Host. Suppose again that the hypotheses of Example 2 remain valid, save that the mortality of infected hosts increases. The equations then assume the form :

$$\left. \begin{array}{l} x' = \varepsilon x + ny - hx^2 - hxy - \alpha xy \\ y' = -(m + \mu)y - hy^2 - hxy + \alpha xy \end{array} \right\} \quad (15)$$

The qualitative result of the discussion does not differ from Examples 2 and 3. In the case in which

$$\varepsilon(\alpha - h) > (m + \mu)h$$

parasitic reproduction is sufficient to ensure the maintenance of the parasitized group. In the case in which

$$\varepsilon(\alpha - h) < (m + \mu)h$$

the parasitized group disappears, and at the limit

$$\lim_{t \to \infty} x = \frac{\varepsilon}{h}, \qquad \lim_{t \to \infty} y = 0.$$

Example 5. Parasitic Action Increases the Limitative Co-efficients without Affecting the Intrinsic Mortality and Fertility. In this case the equations are

$$\left.\begin{array}{l} x' = \varepsilon x + ny - h_{11}x^2 - h_{12}xy - \alpha xy \\ y' = -my - h_{21}xy - h_{22}y^2 + \alpha xy \end{array}\right\} \quad (16)$$

These equations are more complicated than the preceding ones, but the result is the same. There are always two results. In the case in which

$$\varepsilon(\alpha - h_{21}) > mh_{11}$$

the co-existence of the two groups is possible, and the limiting values of x and y are not zero. On the other hand, when

$$\varepsilon(\alpha - h_{21}) < mh_{11}$$

we have in the limit

$$\lim_{t \to \infty} x = \frac{\varepsilon}{h_{11}}, \qquad \lim_{t \to \infty} y = 0.$$

In these four examples we have considered the possible influence of parasitism on all the vital co-efficients. The result is the same in every case. Parasitic activity is not sufficient to exterminate the hosts directly, but it weakens them both physically and numerically. This weakening may disturb the equilibrium which was possible between the given species and its environment, and may lead to its disappearance if its numbers fall below a certain critical value.

3. MULTIPLE PARASITISM

Multiple parasitism may arise in several ways—either by multiple contamination or by multiplication of the parasite within the host. The two cases have a

different mathematical aspect, but it is not always easy to distinguish them, and the simple criteria that are often recommended are not very certain.

Multiple Contamination. Suppose, first, that multiple parasitism is due to multiple contamination. Let x be the total number of hosts, x_k the total number of hosts with k parasites, $p = \sum_{k=1}^{\infty} kx_k$ the total number of parasites, $q = \sum_{k=1}^{\infty} x_k$ the number of infected hosts.

Suppose that the adult parasites are unable to lead a free life, but that their larvae live for a comparatively short time in the environment and penetrate the hosts as they chance to meet them. Choose the unit of time so that no host can be infected more than once per unit. In these circumstances the differential equations may be given the following form:

$$\left. \begin{aligned} x'_0 &= \sum_{s=0}^{\infty} n_s x_s - m_0 x_0 - c_0 p x_0 - x_0 \sum_{s=0}^{\infty} h_{0s} x_s \\ x'_k &= - m_k x_k - c_k p x_k + c_{k-1} p x_{k-1} - x_k \sum_{s=0}^{\infty} h_{ks} x_s \end{aligned} \right\} \quad (17)$$

The contamination co-efficients c_k are not the same for all the groups. When immunity follows contamination the co-efficients form a diminishing series. In the case of parasitic enfeeblement of the hosts the co-efficients form an increasing series. The mortality of the parasites within the bodies of the hosts is neglected.

Suppose that the biological system that is being

studied has reached a stationary state. Eliminating x'_k we have, in general,

$$\frac{x_k}{x_{k-1}} = \frac{c_{k-1}p}{c_k p + m_k + \sum_{s=0}^{\infty} h_{ks}x_s} \qquad (18)$$

Suppose that the presence of the parasites weakens the hosts and diminishes their resistance to later infections. In this case

$$c_{k-1} < c_k$$

and in these circumstances equation (18) gives

$$x_k < x_{k-1}$$

which implies that the series

$$x_0 \qquad x_1 \qquad x_2 \qquad \cdots \qquad (19)$$

is diminishing, or, in other words, that hosts with k parasites are rarer than hosts with $k - 1$ parasites.

Suppose, on the other hand, that the presence of parasites forms a bar to the entry of other larval parasites, that is to say that

$$c_{k-1} > c_k.$$

In this case it is quite possible that for certain values of k

$$x_k > x_{k-1}$$

and the series (19) loses its diminishing character. It is even possible that in some instances it may be increasing. Hence it is incorrect to state that the absence of reproduction of parasites within the host makes series (19) a diminishing one.

Multiplication of Parasites within the Host. Consider now another case in which there is no multiple

contamination and in which reproduction of the parasite is the sole cause of multiple parasitism. The differential equations now assume a slightly different form

$$
\left.
\begin{aligned}
x'_0 &= \sum_{s=0}^{\infty} n_s x_s - m_0 x_0 - cp x_0 - x_0 \sum_{s=0}^{\infty} h_{0s} x_s \\[2ex]
x'_1 &= - m_1 x_1 - \beta_1 x_1 + cp x_0 - x_1 \sum_{s=0}^{\infty} h_{1s} x_s \\[2ex]
x'_k &= - m_k x_k - \beta_k x_k + \beta_{k-1} x_{k-1} - x_k \sum_{s=0}^{\infty} h_{ks} x_s
\end{aligned}
\right\} \quad (20)
$$

The terms $\beta_k x_k$ represent the reproduction of the parasite in the host. Here also two different results may be obtained. It is possible that the presence of many parasites in one host does not prevent them from increasing (Malthusian multiplication). In this case

$$\beta_k > \beta_{k-1}.$$

Then in the stationary state

$$
\frac{x_k}{x_{k-1}} = \frac{\beta_{k-1}}{m_k + \beta_k + \displaystyle\sum_{s=0}^{\infty} h_{ks} x_s} \quad (21)
$$

so that series (19) is decreasing or in other words hosts with k parasites are rarer than hosts with $k - 1$ parasites.

Suppose on the other hand that within the interior of the host the parasites are subject to the same limiting factors as affect any population. In this case

$$\beta_k < \beta_{k-1}$$

L

and it may happen that for certain values of k

$$x_k > x_{k-1}$$

so that series (19) loses its diminishing character. It would therefore be incorrect to state that the absence of multiple contamination does not allow series (19) to diminish.

These simple considerations show how much care is necessary when we wish to draw conclusions as to the nature of multiple parasitism from the numerical aspect of the distribution of parasitized hosts. If series (19) is diminishing a choice may be made between multiple contamination facilitated by an enfeeblement of the hosts and unlimited multiplication of the parasites within the host. If the series is not diminishing a choice exists between increasing immunity of the host and limited multiplication of the parasites within. It may be pointed out that simultaneous action of two factors may further complicate the position and make the choice impossible.

We shall take a few examples which will allow a better appreciation of the influence of different factors.

Example 1. Internal multiplication does not occur. The parasites do not affect the vital coefficients.

Equations (17) assume the form:

$$x'_0 = nx - mx_0 - cpx_0 - hxx_0 \tag{22}$$

$$x'_k = -mx_k - cpx_k + cpx_{k-1} - hxx_k \tag{23}$$
$$(k = 1, 2, \dots)$$

The sum of these equations is equal to

$$x' = (n - m)x - hx^2 \tag{24}$$

which shows that all the groups together satisfy the logistic equation. On adding the same equations multiplied by $1, 2, 3, \ldots$, we get

$$p' = p[-m + (c - h)x] \qquad (25)$$

The solution of equation (24) is

$$x = \frac{a(n - m)e^{(n-m)t}}{n - m - ha + hae^{(n-m)t}} \qquad (26)$$

where a denotes the original value of x. We also get

$$p = p(o)e^{-mt}\left[1 - \frac{ha}{n - m} + \frac{ha}{n - m}e^{(n-m)t}\right]^{\frac{c - h}{h}} \qquad (27)$$

The total number of hosts tends towards the limit

$$\lim_{t \to \infty} x = \frac{n - m}{h}.$$

As far as the distribution of the parasites is concerned, two possibilities have to be considered. In the first case we have

$$c(n - m) > nh$$

and the total number of parasites increases indefinitely; it is clear that this state of affairs is biologically impossible, for if parasites become more and more numerous they end by upsetting their hosts, and the vital co-efficients will change in such a way that the problem will be completely different. In the second case we have

$$c(n - m) < nh;$$

the number of the parasites approaches zero, as does all x_k except x_0, which approaches $\dfrac{n - m}{h}$, and as a

result the hosts rid themselves of their parasites. The inequalities

$$c(n - m) \gtreqless nh$$

lend themselves to many biological interpretations, which may be expressed in any case in accordance with the peculiarities of the species under consideration.

In the following examples we shall study the effect of the disadvantage due to the parasites, in the absence of any internal multiplication.

Example 2. The parasites modify the co-efficients of mortality and of meeting the host.

Suppose that parasitic action modifies the mortality and meeting co-efficients in the following way:

$$m_0 = m, \quad m_k = m + \theta, \quad (k = 1, 2, \ldots)$$

$$h_{0s} = \lambda, \, h_{ks} = \lambda + \mu, \, (k = 1, 2, \ldots, s = 0, 1, 2, \ldots$$

The co-efficients of fertility and contamination remain unchanged. In these circumstances equations (17) become

$$x'_0 = nx - mx_0 - cpx_0 - \lambda x_0 x \qquad (28)$$

$$x'_k = -(m + \theta)x_k - cpx_k + cpx_{k-1} - (\lambda + \mu)xx_k$$
$$(k = 1, 2, \ldots) \qquad (29)$$

From these we get

$$p' = p[-(m + \theta) + (c - \lambda - \mu)x] \qquad (30)$$

$$x' = (n - m - \theta)x - (\lambda + \mu)x^2 + \theta x_0 + \mu xx_0 \quad (31)$$

The three equations (28), (30), and (31) enable us to evaluate the three functions x_0, x, and p. We here limit ourselves to the equilibrium state. Two possibilities are to be considered. In the first case we have the inequality

$$c - \lambda - \mu < 0;$$

the function p decreases and approaches zero, which means that the variables $x_1, x_2, \ldots$, also tend towards zero; the host rids itself of parasites, and finally

$$\lim_{t \to \infty} x = \lim_{t \to \infty} x_0 = \frac{n - m}{\lambda}.$$

In the second case we have

$$\left.\begin{array}{l} c - \lambda - \mu > 0 \\ (c - \lambda - \mu)(n - m) > \lambda(m + \theta) \\ c(m + \theta) > n(c - \lambda - \mu) \end{array}\right\} \qquad (32)$$

Equations (28–29) give the following equilibrium values

$$X = \frac{m + \theta}{c - \lambda - \mu}$$

$$P = \frac{(m + \theta)[(n - m)(c - \lambda - \mu) - \lambda(m + \theta)]}{(c - \lambda - \mu)[c(m + \theta) - n(c - \lambda - \mu)]}$$

$$X_0 = \frac{(m + \theta)[c(m + \theta) - n(c - \lambda - \mu)]}{(c - \lambda - \mu)[\mu(m + \theta) + \theta(c - \lambda - \mu)]}$$

$$X_k = \frac{c^k P^k X_0}{[m + \theta + cP + (\lambda + \mu)X]^k} = \frac{P^k X_0}{(P + X)^k}$$

Thus the values of X_k form a geometrically decreasing series, which, in certain cases corresponds closely with observation. The equilibrium is stable and the process tends towards it when the inequalities (32) are satisfied. In this case co-existence of healthy and infected hosts is possible.

The following examples serve to show that in the case of a progressive increase in the co-efficients of mortality and the limiting co-efficients the only possible results are either the co-existence of the groups x_0,

$x_1, x_2, \ldots$, or the complete extinction of the parasitized groups.

Example 3. The parasites progressively change the limiting co-efficients.

To fix our ideas, suppose that the parasitic action is expressed by an arithmetical progression of the limitative co-efficients:

$$h_{ks} = \lambda + \mu k.$$

Equations (17) become

$$x'_0 = nx - mx_0 - cpx_0 - \lambda x_0 x \qquad (33)$$

$$x'_k = - mx_k - cpx_k + cpx_{k-1} - (\lambda + k\mu)xx_k$$

$$(k = 1, 2, \ldots) \qquad (34)$$

These equations give first

$$x' = (n - m)x - \lambda x^2 - \mu px \qquad (35)$$

Two stationary states are possible. In the first case we have

$$\mu P + \lambda X = n - m$$

$$\frac{X_k}{X_{k-1}} = \frac{cP}{m + cP + (\lambda + km)X} < 1$$

$$X_0 = \frac{nX}{m + cP + \lambda X}$$

which enables X_k to be expressed in terms of P

$$X_k = \frac{n(n - m - \mu P)\lambda^k c^k P^k}{[\lambda n + \lambda P(c - \mu)] \prod_{s=1}^{k} [\lambda n + \lambda(c - \mu)P + s\mu(n - m - \mu P)]}$$

$$(k = 1, 2, \ldots) \qquad (36)$$

Replacing X_k by these expressions in the equations

$$p = \sum_{k=1}^{\infty} k x_k$$

we get, to determine P, the equation

$$P = \frac{n(n-m-P)}{\lambda n + \lambda(c-\mu)P} \sum_{k=1}^{\infty} \frac{k \lambda^k c^k P^k}{\prod\limits_{s=1}^{k} [\lambda n + \lambda(c-\mu)P + s\mu(n-m-\mu P)]} \quad (37)$$

The values of P with which we are concerned must lie within the limits $\left(0, \dfrac{n-m}{\mu}\right)$, for otherwise x_k would have negative values, which is impossible. The right-hand side of equation (37) disappears when $p = 0$ or when $p = \dfrac{n-m}{\mu}$. Hence it passes through a maximum in the interval $\left(0, \dfrac{n-m}{\mu}\right)$. Equation (37) has certainly one root other than zero in this interval if the inequality

$$\lambda n < (c-\mu)(n-m) \quad (38)$$

is satisfied. This inequality may be interpreted in several ways; it may be said, for instance, that the contamination of the hosts expressed by the co-efficient c is a factor which is opposed to the destructive tendencies represented by the limitative co-efficients λ and μ. Suppose that the inequality (38) is satisfied and let P be the first root, other than zero, of equation

(37). The first stable stationary state of the system is expressed by the values

$$p = P, \quad x_0 = \frac{n(n - m - \mu P)}{\lambda n + \lambda P(c - \mu)}$$

and by formula (36). The series x_k is decreasing.

Suppose on the contrary the inequality (38) is not satisfied. Then the system

$$p = 0, \ x_0 = x = \frac{n - m}{\lambda}, \quad x_1 = x_2 = \ldots = 0$$

represents the second stable stationary state in which the factors favourable to the parasites are not sufficient to ensure the existence of parasitized groups.

Example 4. Progressive increase in the co-efficient of mortality.

Suppose that the co-efficient of mortality takes the form

$$m_k = m + \theta k$$

and that the other vital co-efficients are unaffected. Equations (17) become

$$x'_0 = nx - mx_0 - cpx_0 - hx_0x \qquad (39)$$

$$x'_k = - (m + k\theta)x_k - cpx_k + cpx_{k-1} - hxx_k$$
$$k = 1, 2, \ldots) \qquad (40)$$

The equilibrium state of this system is given by the equations

$$\theta p = x(n - m - hx), \qquad (41)$$

$$x_0 = \frac{nx}{m + cp + hx}, \ x_k = \frac{c^k p^k x_0}{\prod\limits_{s=1}^{k} (cp + hx + m + s\theta)}$$

Substituting these expressions in the formula

$$p = \sum_{s=1}^{\infty} s x_s$$

we get

$$p = \frac{nx}{m + cp + hx} \sum_{k=1}^{\infty} \frac{kc^k p^k}{\prod_{s=1}^{k} (cp + hx + m + s\theta)} \qquad (42)$$

Equations (41) and (42) enable p and x to be determined. In the case in which

$$h(\theta + n) > c(n - m)$$

there is the stationary stable state

$$x = x_0 = \frac{n - m}{h}, \; p = 0, \; x_k = 0, \; (k = 1, 2, \ldots)$$

In the case in which

$$h(\theta + n) < c(n - m)$$

there is a stable state of equilibrium with p equal to the first root, other than zero, of equation (42).

Thus, continued elimination of contaminated hosts is the only means of protecting a population against an indefinitely increasing contamination. In every case an infected population can rid itself of parasites by a suitable modification of the vital co-efficients.

Example 5. Pagurus and Chlorogaster. We shall end this chapter by a study of the only case of parasitism for which we have exact figures. It is the case of the Pagurus parasitized by Chlorogaster. These are rhizocephaloid crustaceans, generally presenting several external visceral sacs on each infested Pagurus. Each sac has its own system of apparently independent roots.

C. Perez examined more than two thousand Pagurus and worked out a formula for the distribution of the visceral sacs on infested Pagurus. According to his anatomical studies the hypothesis of multiple con- ·tamination may be disregarded, and there remains the hypothesis of reproduction of the parasite within the host. Here there is a choice between two possi- bilities, limited multiplication or unlimited multipli- cation of the parasites. Only the former can give a non-decreasing distribution of parasites. In the cases observed by Perez the distribution is not decreasing and hence the multiplication of visceral sacs is limited. The internal multiplication of parasites may occur in several ways:

1. It may be supposed that the original infection was due to a single larva, but that the parasitic mass, after becoming internal, was subdivided precociously into a number of independent fragments, which have then developed simultaneously.

2. It may be supposed that the parasitic mass produced by inoculation with a single larva remains itself undivided and gives rise to a continuous root system, a long-lived stock from which successive groups of external sacs are budded off by discontinuous growth. As a result of his most recent anatomical studies of contaminated Pagurus, Perez has adopted this hypo- thesis of budding.

Admitting the hypothesis of budding, suppose that there is some relation between the number of sacs and the age of the host. Let u be the age of a parasite. This age is always less than that of the host. Thus, if the number of sacs increases with the age of the parasite, the Pagurus which carry the greatest number

of sacs are on the average the oldest. Let N_o be the total number of contaminated hosts and $N_o\phi(u)du$ the number of parasites of age $(u,\ u+du)$. This number decreases in accordance with the mortalities of Pagurus and of the parasites. Denote the combined co-efficient of mortality by $x(u)$; then evidently

$$x(u) = -\frac{\phi'(u)}{\phi(u)}, \quad \phi(u) = \phi(0)e^{-\int_0^u x(s)ds}$$

Now bring in the frequency function of the parasites

$$N_o\phi(u)\psi(u,\ p)\ du\ dp$$

in respect of age u and number of sacs p. This function, which gives us the number of parasites with $(p,\ p+dp)$ visceral sacs having an age $(u,\ u+du)$ is wholly analogous to the functions used in demographic statistics. Let the function $\psi(u,\ p)$ take the form

$$\psi(u,\ p) = \frac{1}{\beta(u)}\ V\left(\frac{p}{\beta(u)}\right).$$

Denote by $N(p)dp$ the number of Pagurus carrying $(p,\ p+dp)$ sacs. Then

$$N_o = \int_0^\infty N(p)dp, \qquad 1 = \int_0^\infty V(p)dp.$$

From this the integral equation easily follows:

$$N(p) = N_o\int_0^\infty \frac{\phi(u)}{\beta(u)}\ V\left(\frac{p}{\beta(u)}\right)du$$

which makes it possible to determine the frequency function if all the other functions are known. In fact, we get

$$V(p) = \frac{p}{2\pi p}\int_{-\infty}^\infty p^{-iz}F(z)dz$$

putting

$$F(z) = \frac{\displaystyle\int_0^\infty N(p)p^{iz}\, dp}{\displaystyle\int_0^\infty \phi(u)[\beta(u)]^{iz}\, du}.$$

The functions $\beta(u)$ and $x(u)$ are unknown. Give them an arbitrary but possible form

$$x(u) = B\eta u^{\eta-1}, \qquad \beta(u) = Au^a$$

On the other hand the empirical function

$$N(p) = \frac{N(P)\dfrac{n}{m}\left(\dfrac{p}{P}\right)^m}{\left(\dfrac{p}{P}\right)^n + \dfrac{n-m}{m}}$$

represents very well the observed distribution of the parasitic sacs, P being the number of sacs to which the maximum of $N(p)$ corresponds. As the following table shows, the approximation is sufficiently exact. The parameters taken are:

Males $n = 7$ $m = 1.75$ $P = 5.0$ $N(P) = 29$

Females $n = 7$ $m = 1.75$ $P = 4.5$ $N(P) = 31$

Taking n as equal to $\dfrac{\eta}{\varepsilon}$ and m as $\dfrac{1-\varepsilon}{\varepsilon}$ there is no difficulty in calculating the functions $V(p)$ and $\psi(u, p)$. We get

$$\psi(u, p) = \text{const}\ \frac{[\beta(u)]^{n-m-1}\exp\left\{-\dfrac{n-m}{m}[\beta(u)]^n p^{-n}\right\}}{p^{n-m}}.$$

$\dfrac{p}{N(p)}$	$N(p)\,\male$		$N(p)\,\female$		$N(p)$ Total	
	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.
1	4	2·3	2	3·0	6	5·3
2	7	7·8	10	10·0	17	17·8
3	9	15·7	17	20·0	26	35·7
4	24	24·5	30	29·3	54	53·8
5	29	29·0	29	29·3	58	58·3
6	25	24·2	17	19·5	42	43·7
7	11	15·5	7	10·8	18	26·3
8	10	8·8	5	5·7	15	14·5
9	6	5·1	—	3·2	6	8·3
10	3	3·0	2	1·9	5	4·9
11	2	1·9	—	—	—	—

This is one of Pearson's frequency curves; qualitatively it corresponds well to the probable distribution of Pagurus in respect of u and p, if it be admitted that the number of sacs increases with age up to a certain limit. From this the distribution according to Perez follows immediately. Consequently the hypothesis of single contamination supplemented by a hypothesis of limited budding is well able to explain the facts.

CHAPTER XI

GROWTH OF ORGANISMS

1. General Considerations

By a natural and simple generalization an organism may readily be compared to an animal or vegetable population, such as has been studied in the preceding chapters; the cells, and sometimes the organs, are considered as almost independent elements. It is indeed possible to make up a series connecting the two extremes, and it is very difficult to point to the exact place of separation between the two phenomena. However, this impossibility only means that the two extremes are blended and that the same laws govern the numerical increase of a population without social organization, composed of wholly independent individuals, as govern that of a higher organism with many complex organizations. It may happen that, in a first approximation, the two may be represented by similar equations, but it is certain that neither a second approximation nor the interpretation of the vital co-efficients will be the same. There is not, in fact, a demographic analogy even between populations with different social organizations. A primitive society, almost anarchical and almost homogeneous, may be compared to a rarified gas. A modern society, capitalist or socialist, more closely resembles a very dense, heterogeneous, viscous fluid, with well defined currents, obeying a set of laws and forces unknown to the other, but the most important difference consists in the

existence of a division of labour, and of special organs for social functions. In an animal population, each individual defends and provides for himself according to his needs, a cell in an organism shares in the life of the whole, receives food, and is relieved of its metabolic products. The food necessary for a population is proportional to the number of individuals; in an organism the food needed is proportional neither to the number of cells nor to the weight of the body. The same is true of all relations with the external environment; for an animal or vegetable population the exchanges are proportional to the number of individuals, while for a warm-blooded animal they are proportional to its surface area. The capacity for reproduction in an animal or vegetable population belongs to all individuals,* but this is not true of the cells of an organism. In short, the difference between the two types is not a quantitative but a qualitative one, and the dialectic passage from quantity to quality is real, palpable, and undeniable.

The Development of Multicellular from Unicellular Organisms. The successive stages in the evolution of multicellular from unicellular organisms can be reconstructed. The beginning of the process must have been symbiosis resulting from imperfect separation after conjugation. Incomplete separation reduces the total area of the two bodies and diminishes their exchanges with the environment. In some circumstances this reduction is an advantage, particularly among Protozoa with a specialized surface. The formation of chains, resulting from division unaccompanied by separation,

* I exclude animal societies such as the beehive and the white ants' nest, which require separate treatment.

may sometimes be seen among the Ciliata. By a modification of the physico-chemical conditions the complete separation of a multicellular organism at the beginning of its formation may be artificially produced. Among a variety of environmental conditions it is certain that a favourable situation will be found in some more or less isolated spots. The work of selection has done the rest. In multicellular organisms thus formed specialization of cells is inevitable, and the first specialization is a differentiation between external and internal cells, or sometimes between upper and lower cells. At the same time retardation and localization of certain functions can be seen. Thus a *Stylonychia* undergoes about five divisions a day, but the multiplication of the cells of an organism is subject to a slower rhythm. Further, the capacity for growth is not found in the same degree in all parts of an organism; among plants it is strictly localized, among animals localization is less pronounced but nevertheless it still exists.

Function of External Surface. In the life of a population the frontier plays a minor part; it is in the inside that nourishment takes place, and in constructing equations one only takes account of the movements of immigration and emigrations, which give several complementary terms, the analytical nature of which is analogous to that of the fundamental terms. In an organism, on the contrary, immigration and emigration of cells can scarcely be conceived, while currents of nutritive matter and of energy are of first importance. This fact suggests that the fundamental expenditure in warm-blooded animals, that is to say the energy necessary to maintain the body at a constant temperature is proportional to the area. This *law of surface*

area has been satisfactorily verified by experiment. But functional expenditure is not proportional to the area. Again, the utilization of food in an organism is governed by special laws, at present imperfectly known, but which in no case result in a proportional relation between the food and the energy produced by its consumption.

Constructive Expenditure. Besides the basal expenditure and the functional expenditure, the expenditure necessary for construction must be considered, that is to say the difference between the number of cells reconstituted and destroyed in unit time. The expenditure of energy necessary to account for this difference is very small in comparison with the other two, but its results are important. The constructive potentiality of an organism depends, first, on glandular activity, secondly, on the accumulation of metabolic products in the body, thirdly, on the local retarding action, or in other words, the density of the cell-population, and fourthly, on the localization of cell-division. All these factors vary with the age of the organism. The organs of internal secretion do not come into activity simultaneously. Food varies with age, both as regards quality and quantity : in mammals the period of lactation is very different from the rest of their lives. The intervention of the sex glands profoundly modifies the vital co-efficients of an organism. The accumulation of metabolic products with a consequent degeneration of tissues leads first to a retardation of growth and then to the dissolution of the organism. Finally, in addition to these accelerating or retarding factors the external form of the organism must be taken into account. The development of form

M

in its turn obeys laws which are doubtless simple but which are hitherto unknown. A few statements of fact, chiefly of a negative character, are of interest. First, the growth of an organism does not occur simultaneously in all directions. The old observation that a man grows first in height, then in breadth, and finally in "bulk" applies *mutatis mutandis* to all organisms. It follows therefore that at different times in life growth is not proportional either to weight or to area or to stature. Is it proportional to some power of the weight w^m? If so the exponent m depends on the age and perhaps also on the weight.

$$m \sim m(t, w).$$

The same is true of all other biological characters and factors.

Growth Problems expressed as Equations. The final result of this discussion may be summarized as follows:

1. The development of an organism or even the growth of any bodily character cannot be represented by a single equation or a single formula.

2. The process must be divided into several parts (for instance, for man; embryonic stage, breast-feeding, infancy, adolescence, sexual maturity, old age) and each part must be represented by the appropriate equation.

3. It may be supposed that numerical characteristics of any part of the body whatever are linked with the weight w by a relation of the type

$$x \sim w^m$$

4. Hence each stage of increase of weight can be represented by the integro-differential equation

$$w' = \varepsilon_s w^{k_s} - h_s w^{l_s} - c_s w^{m_s} \int_{t_{s-}}^{t} w^{n_s}(u)du \quad (t_{s-1} < t < t_s) \ (1)$$

with a suitable choice for each stage of the co-efficients ε_s, h_s, c_s, and the indices k_s, l_s, m_s, n_s, and also of the initial and final moments.

5. In this equation the term $\varepsilon_s w^{k_s}$ expresses the whole of the constructive activities, the term $h_s w^{l_s}$ expresses the whole of the retarding activities and the integral term expresses the residual activities.

This form of the equation is not very precise, nevertheless it expresses the antagonistic influences which act upon an organism during its growth.

Insufficiency of Biological Statistics. A few more words are necessary on the numerical data of biology. In all biological statistics serious methodological defects are to be found. Thus in data concerning the growth of animals, each average is deduced from a different number of animals, which makes some publications, full of figures and very expensive, altogether useless.

A deplorable error is to be found concerning feeding and metabolism in animals. Express the weight, the metabolism, and the food consumed by an animal each day as a function of its age:

Weight $= f(t)$; metabolism $= \phi(t)$; food $= \psi(t)$.

Eliminating t from any two of these we get equations of the type

Metabolism $= F(w)$; Food per day $= \Phi(w)$.

Again, from observations of animals of the same age but different weights, relations between the same biological variables can be deduced.

Metabolism $= F_1(w)$; Food per day $= \Phi_1(w)$.

but this does not mean that

$$F(w) \equiv F_1(w). \qquad \Phi(w) \equiv \Phi_1(w).$$

In reality these functions are completely different. This circumstance is often forgotten. The true relation between weight and metabolism of an animal is given by the function F_1 and not by F.

Growth-curves of animals possess a truly remarkable peculiarity. Save for man, these curves never pass through a maximum. This means that only the ascending portion of the life of an animal has been observed, as if there were no aged animals in existence. It seems that this is due to the extreme vulnerability of animals in natural circumstances. Hence, contrary to the general opinion, natural conditions are wholly unfavourable for animals, and it is to civilization that man owes the descending portion of his growth curve.

2. UTILIZATION OF FOOD BY AN ORGANISM

A simple relation can be deduced between the food absorbed by an animal and its utilization. This relation gives a plausible explanation of the empirical law deduced by S. Brody and R. C. Procter. It concerns the relation between the net energy x taken in by an organism and the gross energy X absorbed as food. According to Brody and Procter this relation is expressed by the following formula:

$$x = A(1 - e^{-mX}) \tag{2}$$

I shall show that this formula can be replaced by another equally simple and corresponding equally well with the observations, but based on a few almost evident premisses which permit a wider range of application.

Suppose that the utilization of large and small

amounts of alimentary energy do not obey the same laws and that the two gross amounts of energy A and B which separately produce the net energies a and b give, acting in conjunction, the net energy

$$\frac{a + b}{1 + k^2ab} < a + b.$$

Denote by the sign $(+)$ the operation of physiological synthesis so that

$$A(+)B = \frac{a + b}{1 + k^2ab} \qquad (3)$$

If A and B are very small, we get approximately

$$A(+)B \simeq a + b \qquad (4)$$

and the net energy a derived from the gross energy A is proportional to A

$$a = \sigma A \qquad (5)$$

In the same way the symbolical operations of subtraction, multiplication, and division can be interpreted. Multiplication is the only one that concerns us here. We find easily

$$A(+)A = 2(\times)A = \frac{2a}{1 + k^2a^2}$$

$$2A(+)A = 3(\times)A = \frac{\dfrac{2a}{1 + k^2a^2} + a}{1 + k^2 \dfrac{2a}{1 + k^2a^2} a} = \frac{3a + k^2a^3}{1 + 3k^2a^2}$$

Put $\qquad\qquad n(\times)A = \dfrac{P_n(a)}{Q_n(a)} \qquad\qquad (6)$

It is easy to see that the polynomials $P_n(a)$ and $Q_n(a)$ satisfy the following relations

$$\left. \begin{array}{l} P^{n+1}(a) = P_n(a) + aQ_n(a) \\ Q^{n+1}(a) = Q_n(a) + k^2aP_n(a) \end{array} \right\} \qquad (7)$$

and also that

$$P_n(a) = -P_n(-a), \qquad Q_n(a) = Q_n(-a). \qquad (8)$$

Equations (7) give

$$kP_n(a) + Q_n(a) = (1 + ka)^n \qquad (9)$$

which, taken together with (8) permits $P_n(a)$ and $Q_n(a)$ to be evaluated

$$\left. \begin{array}{l} P_n(a) = \dfrac{(1 + ka)^n - (1 - ka)^n}{2k} \\[3mm] Q_n(a) = \dfrac{(1 + ka)^n + (1 - ka)^n}{2} \end{array} \right\} \qquad (10)$$

and we get finally

$$n(\times)A = \frac{(1 + ka)^n - (1 - ka)^n}{k[(1 + ka)^n + (1 - ka)^n]} \qquad (11)$$

Suppose that A and a are small and n is large. Replace a by σA, A by $\dfrac{X}{n}$, $n(\times)A$ by x. The preceding formula becomes

$$x = \frac{1}{k} \lim_{n \to \infty} \left[\frac{\left(1 + \dfrac{k\sigma X}{n}\right)^n - \left(1 - \dfrac{k\sigma X}{n}\right)^n}{\left(1 + \dfrac{k\sigma X}{n}\right)^n + \left(1 - \dfrac{k\sigma X}{n}\right)^n} \right]$$

or

$$x = \frac{1}{k} \frac{e^{k\sigma X} - e^{-k\sigma X}}{e^{k\sigma X} + e^{-k\sigma X}} = \frac{1}{k} th(k\sigma X) \qquad (12)$$

When k is small enough equation (5) reappears.

The maximum possible value of the net energy is $\frac{1}{k}$. The form of curve (12) is the same as that of curve (2) and curve (12) represents the numerical data of Brody as well as curve (2).

One important point remains to be cleared up—the dependence of the co-efficients k and σ on the weight of the animal. It may be expected *a priori* that the digestibility of food will not be the same for animals of different weights. Brody's figures and equation (12) suggest a solution of this problem. The following figures relating to the cattle of Illinois (Ill. Steer B in Brody's notation) exist:

Average weight $= 613$ kg., $\frac{1}{k} = 38,500$, $\sigma k = \cdot 0000126$ which give

$$\sigma = \cdot 48, \qquad \frac{1}{kw} = 63.$$

The figures for another breed (Steer 36 PA) are:

Average weight $= 433$ kg., $\frac{1}{k} = 24,000$, $\sigma k = \cdot 0000195$ whence

$$\sigma = \cdot 47, \qquad \frac{1}{kw} = 56.$$

This result is most interesting. The co-efficient σ is a physical co-efficient which is constant for the different breeds of a species, and its constancy is an encouraging confirmation of our theory. It is further seen that the maximum assimilated energy is proportional to the weight of the animal, and that therefore:

$$\frac{1}{k} = \alpha w \tag{13}$$

which in a general sense confirms the observations.

In these conditions, formula (12) becomes

$$x = \alpha w th\left(\frac{\sigma X}{\alpha w}\right) \tag{14}$$

Two extreme cases may appear. In the first $\dfrac{\sigma X}{\alpha w}$ is so small that the hyperbolic tangent can be replaced by its argument, which gives the relation between x and X

$$x \simeq \sigma X; \tag{5'}$$

and in this case the weight of the body does not explicitly appear, and the net energy depends on w only by the intervention of X. In the second case $\dfrac{\sigma X}{\alpha w}$ is so great that the hyperbolic tangent may be replaced by.1, which gives

$$x \simeq \alpha w \tag{15}$$

that is to say that the net energy obtained by an animal from a very abundant food-supply is proportional to the weight of its body. The use of these formulae in the theory of the growth of animals will appear later.

3. GROWTH OF TISSUES

B. Ephrussi and G. Teissier have carried out experiments on the growth of tissue cultures, concerning the residual growth of fragments of tissue in a purely protective medium. According to Carrel the residual activity of tissues arises from the small reserve which every fragment of tissue taken from an organism carries with it. Among the factors concerned in the growth of these cultures are two to which the authors attribute a decisive part.

1. The gradual exhaustion of certain substances.

2. The peripheral localization of the majority of the mitoses.

Let s be the area of the culture at the moment t and S the final area when growth is finished. The differential equation of the problem takes the form

$$s' = \mu s^{\frac{1}{2}}(S - s) \qquad (16)$$

which merely implies that growth is proportional to the periphery $s^{\frac{1}{2}}$ and to the available reserves of nutritive material. This reserve can be calculated. At the beginning the fragment of surface area s_0 includes a quantity of reserve material αs_0. At the end of time t the area becomes s and this growth is accompanied by a consumption of the reserves proportional to the increase of area $s - s_0$. The amount of reserve e which remains available at the time t will then be equal to

$$e = \alpha s_0 - \beta(s - s_0) = (\alpha + \beta)s_0 - \beta s.$$

Hence

$$S = s_0 \frac{\alpha + \beta}{\beta}$$

Integration of equation (16) gives

$$s = S\left[\frac{(\sqrt{S} + \sqrt{s_0})e^{\mu\sqrt{S}} - (\sqrt{S} - \sqrt{s_0})}{(\sqrt{S} + \sqrt{s_0})e^{\mu\sqrt{S}} + (\sqrt{S} - \sqrt{s_0})}\right] \qquad (17)$$

To simplify this, put

$$S = s_0\lambda^2, \qquad \mu\sqrt{S} = \varepsilon = \mu\lambda\sqrt{s_0}$$

and

$$\lambda^2 = \frac{\alpha + \beta}{\beta} > 1$$

Equation (17) becomes

$$s = \lambda^2 s_0 \left[\frac{(\lambda + 1)e^{\,et} - (\lambda - 1)}{(\lambda + 1)e^{\,et} + (\lambda - 1)} \right]^2$$

This formula conveniently expresses the experimental data. In particular it shows that for two tissues characterized by the same co-efficient λ the final areas are proportional to the initial areas. This proportionality does not exist during growth because of the presence of the index ε.

CHAPTER XII

EMBRYONIC GROWTH

1. THE FREE EMBRYO

CONSIDER a free embryo. It may be represented schematically as a whole containing the *organizer,* of weight w, and its nutritive reserve, of weight n. Suppose, first, that all the changes within this system and between this system and the atmosphere are always proportional to these weights; secondly, that the absorption of food in unit time is equal to $aw + bwn$; thirdly that the constructive utilization of the food in unit time is equal, according to formula (5) of Chapter XI, to $\tau(aw + bwn)$, if it be unnecessary to take account of the set of limitative factors or of intoxication by the products of metabolism; fourthly, that the limitative term is equal to hw^2; and fifthly, that the toxic action is $cw\mathrm{W}$, denoting by W the integral

$$\mathrm{W} = \int_0^t w \, dt.$$

Thus, the equations of the problem assume the form :

$$\left.\begin{array}{l} w' = \tau(aw + bwn) - hw^2 - cw\mathrm{W} \\ n' = -aw - bwn \end{array}\right\} \tag{1}$$

These equations can easily be integrated. The second of equations (1) gives

$$n = \left(n_0 + \frac{a}{b}\right)e^{-b\mathrm{W}} - \frac{a}{b}. \tag{2}$$

Replace n by this expression in the first of equations (1), expressing w' and w in terms of W,

$$W'' + hW'^2 = \tau bW'\left(n_0 + \frac{a}{b}\right)e^{-bW} - cW'W$$

Multiply this equation by e^{hW}

$$(W'' + hW'^2)e^{hW} = \tau(n_0 b + a)W'e^{(h-b)W} - cW'We^{hW}$$

and on integrating we get

$$w = W' = F(W) \tag{3}$$

which gives

$$F(W) = \frac{\tau(n_0 b + a)}{h - b}\left(e^{-bW} - e^{-hW}\right) + w_0 e^{-hW}$$
$$- \frac{c}{h^2}e^{-hW} + \frac{c}{h^2} - \frac{cW}{h} \tag{4}$$

By integrating equation (3) we get the time t as a function of W

$$t = \int_0^W \frac{ds}{F(s)} \tag{5}$$

Thus we have the complete solution of the problem in parametric form. We shall study this solution. Write the equation for the relative growth of the organizer

$$\frac{w'}{w} = \left[\frac{h\tau(n_0 b + a)}{h - b} + \frac{c}{h} - w_0 h\right]e^{-hW}$$
$$- \frac{b\tau(n_0 b + a)}{h - b}e^{-bW} - \frac{c}{h}$$

The theoretical curve has three peculiar points. First, the function $F(W)$ vanishes for a certain value of $W = W_\infty$, which corresponds to $w = 0$; secondly,

the function w' vanishes for a certain value of W $= W_m < W_\infty$, which corresponds to the maximum value of $w = w_m$; thirdly the function n vanishes for a certain value of W

$$W = W_e = \frac{1}{b} \log \left(1 + \frac{n_0 b}{a} \right) \qquad (6)$$

The fate of the system depends wholly on the food-supply.

First Case. It may happen that the initial reserve of food is insufficient so that

$$\tau(n_0 b + a) < w_0 h, \qquad w'(0) < 0 ;$$

the weight of the organizer decreases, and the embryo dies unless metamorphosis occurs before the disappearance of the reserves.

Second Case. The initial reserve is sufficient, so that

$$\tau(n_0 b + a) > w_0 h, \qquad w'_0 > 0 ;$$

the weight of the embryo begins to increase, reaches a maximum and must then tend towards zero. Metamorphosis must be supposed to occur in the neighbourhood of the maximum and to coincide approximately with the moment of disappearance of nutritive reserves. The hypothesis of the simultaneous occurrence of these two phenomena is expressed by the equation $W_e = W_n$, which gives the original weight of the organizer

$$w_0 = \frac{1}{h} \left\{ - \left(\frac{c}{h} + \frac{ab\tau}{h-b} \right) \left(1 + n_0 \frac{b}{a} \right)^{\frac{h}{b}} + \frac{h\tau(n_0 b + a)}{h-b} + \frac{c}{h} \right\} \quad (7)$$

as a function of the reserve of nutritive material n_0.

In this argument it has been assumed that the utilization of the food is complete. Suppose that the reverse is true, and apply formula 15, Chapter XI. This gives a slightly different system:

$$w' = \varepsilon w - h w^2 - c w \mathrm{W}, \quad n' = - a w - b w n \quad (8)$$

The first equation is familiar: it also gives a curve with a maximum. Further, equation (6) gives the the value of W at the moment of total consumption of food. If these two moments are almost coincident, metamorphosis occurs at about this critical time. Thus the two possibilities, equation (5) and equation (15) of Chapter XI, give the same qualitative result.

2. Embryo in the Mother's Body

An embryo that develops in the mother's body lives in totally different circumstances from those of the preceding section. It receives nourishment regularly, and the products of its metabolism are more or less eliminated. In these exchanges surface area does not play so important a part as in the adult condition, and it may be supposed that in the absence of limitative factors the vital balance of the embryo should become positive and proportional to its weight. Food is, in fact, proportional to the weight w. Hence, replacing X by λw in equation (14), Chapter XI, we see that the utilization of the food is proportional to the weight:

$$x = \alpha w \, th \left(\frac{\sigma \lambda}{\alpha} \right)$$

Basal metabolism and metabolism of function are zero and all this energy is used for growth. Thus at the

beginning of embryonic development we return to the Malthusian equation

$$w' = \varepsilon w.$$

This equation must be completed by limitative terms. First, there is a kind of mechanical pressure which increases with the growth of the embryo; further, a certain competition between the cells of the embryo can be foreseen; lastly, it must be supposed that in spite of elimination there are accumulated products of metabolism coming from the embryo itself and from the increasingly disordered maternal tissues. It is extremely difficult to estimate even approximately how great these opposing actions will be. A more or less accurate qualitative representation can be obtained by the equation

$$w' = \varepsilon w - hw^2 - cw\mathrm{W} \tag{9}$$

denoting as usual by W the integral

$$\mathrm{W} = \int_0^t w\, dt$$

We summarize the peculiarities of the solution of equation (9) in the three cases of practical interest to us.

1. In the absence of toxic action, this is the logistic law. When $w(0) < \dfrac{\varepsilon}{h}$ the function w increases and approaches $\dfrac{\varepsilon}{h}$;

2. In the absence of internal competition when $w(0)$ is very small we have, approximately

$$w = \frac{4\varepsilon^4 w(0) e^{\varepsilon t}}{[2\varepsilon^2 + w(0) c e^{\varepsilon t}]^2}; \tag{10}$$

the function w at first increases, reaches a maximum equal to

$$w_m = \frac{\varepsilon^2}{2c} \qquad (11)$$

at the moment

$$t_m = \frac{1}{\varepsilon} \log \frac{2\varepsilon^2}{cw(0)} \qquad (12)$$

and then decreases to zero.

3. In the general case the solution of equation (9) may be represented by the following approximate formulae

$$\left.\begin{array}{ll} w = \dfrac{w(0)w_m}{w(0) + (w_m - w_0)e^{-\varepsilon t}} & (0 < t < t_m) \\[3mm] w = \dfrac{w_m}{ch^2 \dfrac{c(t - t_m)}{2}} & (t_m < 1) \end{array}\right\} \quad (13)$$

denoting the maximum value of w by w_m and the time at which w reaches its maximum by t_m. When h is sufficiently small this time is expressed well enough by formula (12). The maximum value w_m is equal to

$$w_m = \frac{\varepsilon}{h} - \frac{c}{h^2} \log \left[\frac{c + \varepsilon h - h^2 w(0)}{c} \right] \qquad (14)$$

Experimental verification is always very difficult, for the statistical data are always defective and will remain so until a means is found of weighing an embryo without killing it. In averages in which each individual appears once only the dispersion is too great to permit more than qualitative conclusions. We shall examine a few numerical examples.

Example 1. White Rats. For these animals the following statistics exist:

Age (Days)	Weight (Grams)		Age (Days)	Weight (Grams)	
	Observed	Calculated		Observed	Calculated
13	·040	·063	19	1·58	1·64
14	·112	·112	20	2·63	2·54
15	·168	·196	21	3·98	3·68
16	·310	·342	22	4·63	4·73
17	·548	·59	Birth	4·68	—
18	1·000	1·00	—	—	—

Before the thirteenth day the embryos are too small to appear usefully in the table, and for the same reason the figures for the 13th, 14th, and 15th days must be considered doubtful. Some useful conclusions may, however, be drawn. At the beginning, limitative and toxic actions are slight and w is expressed by the Malthusian law

$$w = w(o)e^{\varepsilon t}$$

or, in logarithmic form

$$\log w = \log w(o) + \varepsilon t \tag{15}$$

Consequently, with semi-logarithmic co-ordinates, the beginning of growth may be represented by the straight line (15). If, on the contrary, growth were proportional to the surface area of the body we should have, in the same conditions:

$$w' = \varepsilon w^k + \ldots \qquad \left(k \simeq \frac{2}{3} \right)$$

$$w \simeq [\varepsilon(1 - k)t + w_0{}^{1-k}]^{\frac{1}{1-k}}$$

or, if w_0 is very small

$$w \simeq [\varepsilon(1 - k)t]^{\frac{1}{1-k}}$$

N

and in logarithmic form,

$$\log w \simeq \frac{\log [\varepsilon(1 - k)]}{1 - k} + \frac{\log t}{1 - k} \qquad (16)$$

hence, with logarithmic co-ordinates $\log w$, $\log t$ the beginning of growth would be represented by a straight
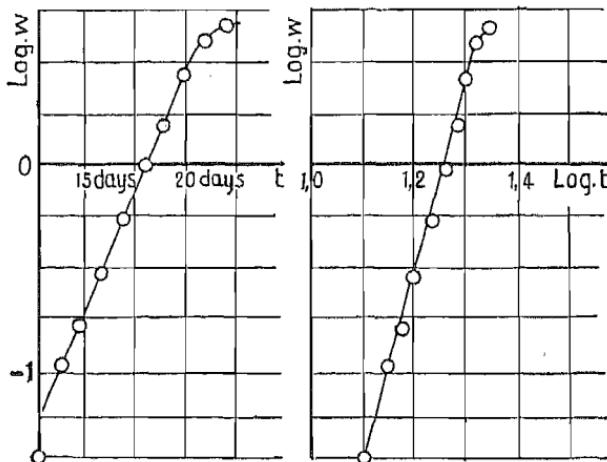

FIG. 10.—EMBRYONIC GROWTH OF THE WHITE RAT

line. For white rats the possibility of equation (15) is realized from the 13th to the 21st day (Fig. 10). The conclusion is that in these animals pure embryonic growth is proportional to the weight of the body and not to its area. The parameter ε and the initial value of w are equal to

$$\varepsilon = \cdot 53; \qquad w_0 = 7 \cdot 10^{-5} \text{ gram.}$$

Consider now the final stage of embryonic growth. Application of the logistic law shows that the hypothesis of the absence of toxic action is inadmissible. In fact

the limitative action only becomes noticeable from the 21st day, but in a most emphatic way, which is inconsistent with the logistic law. Equation (9) may be improved by supposing that internal competition is proportional to a higher power of w.

$$w' = \varepsilon w - h w^{1+m} \qquad (m > 1) \qquad (17)$$

The solution of this equation is

$$w = w(0)e^{\varepsilon t} \sqrt[m]{\frac{\varepsilon}{w_0^{\,m} h e^{\varepsilon m t} + \varepsilon - w_0^{\,m} h}}. \qquad (18)$$

This formula, applied to the case of the white rat, will represent its embryonic growth when m is given a value of at least 2. Possibly justification may be found for putting $m \geqslant 2$, but I do not see it. On the contrary, formula (10), which expresses pure toxic action fairly closely, represents the observed growth-curve. If $c = \cdot 0295$ a satisfactory curve is obtained, reaching a maximum at $t_m = 23\cdot7$ days. The calculated values of w are found in the third column of the table above. Birth must occur a little before the critical point.

Example 2. Rabbits (after Chaine). For the rabbit the following figures exist :

t (days)	14	16	18	20	22	24	26	28	30
w (obs.) .	·16	·37	·94	1·61	5·52	11·0	25·0	40·0	60·0
w (calc.) .	·17	·40	·94	2·17	4·96	11·0	25·4	41·6	59·7

As in the first example, log w is very well represented up to the 26th day by formula (15) with the following values for the parameters

$$w(0) = 5\cdot10^{-4} \text{ gram}; \qquad \varepsilon = \cdot415.$$

Curve (10) reaches its maximum at

$$t_m = 31\cdot6, \qquad c = \cdot0014.$$

Hence, as in the case of the white rat, birth takes place a little before the maximum point. The agreement between observed and calculated values of w is close up to the 18th and after the 22nd days. In the interval, 19th–21st, the deviation is considerable.

Example 3. Guinea Pig (Ibsen and Draper). To show the small degree of certainty that statistical data on growth present we compare the curves of embryonic growth of the guinea pig, which we owe to Ibsen (I) and Draper (D):

Age (days)	20	30	40	50	60	64	67
Weight (grams) I .	·062	1·32	9·4	36·3	62·5	—	96·6
Weight (grams) D .	·080	1·50	10·1	29·9	61·6	84	—

The semi-logarithmic straight lines (15) represent the observations better than the logarithmic straight lines (16), and hence pure embryonic growth is proportional to the weight of the body.

For guinea pigs the limitative actions become noticeable much earlier than for rabbits or white rats (Fig. 11). Also it cannot be affirmed that in this case one or the other of these factors predominates. In both series the co-efficient of multiplication ε is equal to ·11. In the same way

$$h = \cdot0011, \qquad w_0 = \cdot22, \qquad c = \cdot00007$$

but the calculated curve agrees very imperfectly with the observations, especially for small values of t.

The other examples more or less confirm our conclusions, which may be stated thus:

1. Purely embryonic growth in mammals is proportional to the weight of the body and not to its area.
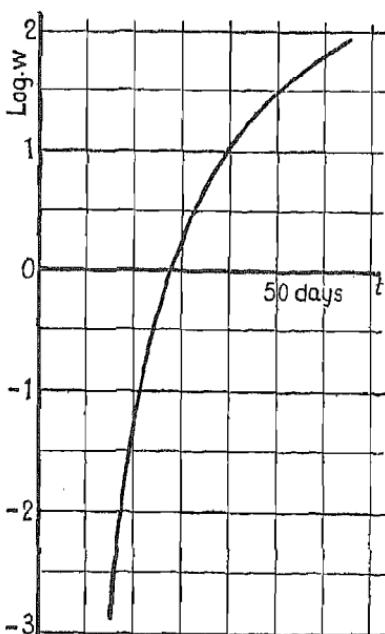

FIG. 11.—EMBRYONIC GROWTH OF
THE GUINEA PIG
after Ibsen and Draper.

2. Equation (9) and its two special cases give good agreement with the observations.

3. In some instances residual action seems to be more important than the action of internal competition.

In this respect it may be remarked that the nature of residual action is not necessarily chemical and that it is quite possible to conceive the accumulation of residual effects of a mechanical or physical nature.

CHAPTER XIII

POST-EMBRYONIC GROWTH

1. Human Growth

In the study of the post-embryonic growth of mammals, metabolism and nutrition must be taken into account far more than in the study of embryonic development. Further, the process must be subdivided into a number of stages, each characterized by the constancy of its vital co-efficients, with a sharp change in the co-efficients on proceeding from one stage to the next. We shall consider first the growth of human beings, and the better to show the existence of the critical points we shall employ the following method. Suppose that the differential equation of growth takes the form

$$w' = F(w) \tag{1}$$

explicitly independent of the time t. Making use of the numerical table of human growth, calculate the values of w' and construct the curve $F(w)$ (Fig. 12).

Consider this curve. During the first eighteen months growth is very rapid; then it becomes slower, doubtless because of the change in diet, and remains at almost the same value until the ninth year. At this point a revival of growth occurs, and increases till the 15th or 16th year: this is the maximum value of w', later it decreases rapidly and disappears at about the thirtieth year. After thirty years w' is negative. The form of

this curve shows that human growth should be divided into several characteristic periods of very different duration.

The first stage, that of breast-feeding, is characterized
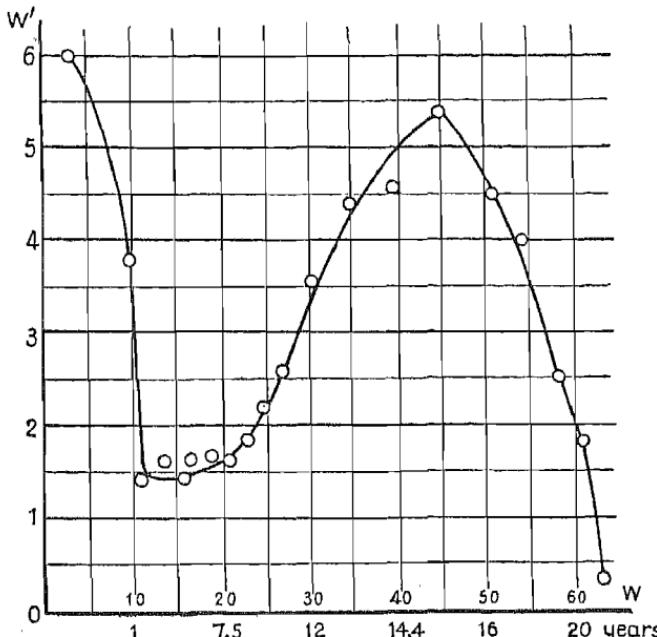
FIG. 12.—FUNCTION $w' = \mathrm{F}(w)$ FOR MAN
after Quételet.

by a very high value of w', and then by a rapid decrease to the level of the next period. From the second to the ninth year the annual increase in weight maintains the same level, with perhaps a slight tendency to increase. Suppose that during this time w' is proportional to some power of w

$$w' = \varepsilon w^k \quad (\text{1·5} < t < 9) \tag{2}$$

HUMAN GROWTH, ACCORDING TO QUÉTELET

Age (Years)	Height (l) (Meters)	Weight (w) (Kilos)	w'	l'	$w^{\frac{1}{3}}$	$\dfrac{w^{\frac{1}{3}}}{l}$
0	·50	3·5			1·518	3·04
1	·70	9·4	3·9	·145	2·110	3·01
2	·79	11·3	1·5	·080	2·244	2·84
3	·86	12·4	1·45	·070	2·315	2·69
4	·93	14·2	1·65	·070	2·422	2·60
5	1·00	15·7	1·5	·055	2·504	2·50
6	1·04	17·2	1·7	·050	2·581	2·48
7	1·10	19·1	1·75	·060	2·673	2·43
8	1·16	20·7	1·75	·060	2·746	2·37
9	1·22	22·6	1·9	·055	2·827	2·32
10	1·27	24·5	2·25	·055	2·904	2·29
11	1·33	27·1	2·65	·055	3·004	2·26
12	1·38	29·8	3·6	·055	3·103	2·25
13	1·44	34·3	4·45	·055	3·248	2·26
14	1·49	38·7	4·65	·055	3·383	2·27
15	1·55	43·6	5·45	·055	3·520	2·27
16	1·59	49·6	4·6	·050	3·674	2·31
17	1·63	52·8	4·1	·040	3·752	2·30
18	1·66	57·8	2·6	·035	3·866	2·33
20	1·67	60·0	1·93	·023	3·915	2·35
25	1·68	62·9	·37	·008	3·977	2·37
30	1·68	63·66	·18	·001	3·994	2·38
40	1·68	63·6	— ·01	·	3·991	2·38
50	1·67	63·4	— ·09		3·99	2·39
60	1·64	61·9	— ·20		3·96	2·41
70	1·62	59·5	— ·21		3·90	2·41
80	1·61	57·8			3·87	2·40
90	1·61	57·8			3·87	2·40

and that the limitative factors are negligible: it is then found that the index k is positive and does not exceed one-third:

$$0 \leqslant k \leqslant \frac{1}{3} \tag{3}$$

How can this value of k be explained? It may be noted that in this respect man does not differ from other mammals. The same phenomenon is found both

in rats and sheep. For the explanation we return to equation (14) of Chapter XI, which expresses the utilization of gross energy X by an animal of weight w.

$$x = \alpha w th\left(\frac{\sigma X}{\alpha w}\right) \tag{4}$$

A part of the net energy is used by the animal in growth. Let x_c be this constructive energy. Suppose that it is related to x by the equation

$$x_c = xf(w) \tag{5}$$

Replacing x by its value from equation (4), we get

$$x_c = \alpha w f(w) th\left(\frac{\sigma X}{\alpha w}\right).$$

Further, w' must be proportional to x_c:

$$w' = \varepsilon w^h = \gamma x_c = \gamma \alpha w f(w) th\left(\frac{\sigma X}{\alpha w}\right)$$

This equation enables us to determine the function $f(w)$

$$f(w) = \frac{\varepsilon w^{h-1}}{\gamma \alpha th\left(\dfrac{\sigma X}{\alpha w}\right)} \tag{6}$$

Two extreme cases may be considered. When $\dfrac{\sigma X}{\alpha w}$ is small, equation (6) gives

$$f(w) = \frac{\varepsilon w^h}{\sigma \gamma X}, \tag{7}$$

and when $\dfrac{\sigma X}{\alpha w}$ is large, we get

$$f(w) = \frac{\varepsilon w^{h-1}}{\gamma \alpha}. \tag{8}$$

Suppose that the gross energy X is proportional to w^m, where m lies between $\frac{2}{3}$ and 1: equation (7) can be rewritten as:

$$f(w) = Ew^{k-m} \tag{7'}$$

and there are the inequalities

$$0 < k < \frac{1}{3}, \qquad \frac{2}{3} < m < 1.$$

Consequently the two equations (7) and (8) can be replaced by one

$$f(w) = Hw^{-n} \tag{9}$$

in which n satisfies the inequality

$$\frac{1}{3} < n < 1. \tag{10}$$

Thus, supposing the constructive portion of x to be inversely proportional to a power of w varying from $\frac{1}{3}$ to 1 (linear growth—superficial growth—cubical growth), we get an explanation of the value of k within the limits of expression (3).

The following explanation may also be suggested. According to the experiments of Ephrussi and Teissier on the residual growth of tissues, the hypothesis of peripheral growth is in good agreement with the observations. It is admitted that this hypothesis may also be valid for non-residual growth. In this case the relation between the constructive energy x_c and the net energy x may be expressed by the equation:

$$\frac{x_c}{x} = f(w) = \lambda w^{-\frac{1}{3}} \tag{11}$$

or, replacing x by its value in equation (4):

$$x_c = \lambda \alpha w^{\frac{1}{3}} th\left(\frac{\sigma X}{\alpha w}\right).$$

When $\dfrac{\sigma X}{\alpha w}$ is very small this formula becomes

$$x_c \sim \lambda \sigma X w^{\frac{1}{3}} \sim A w^{m-\frac{1}{3}} \qquad \left(\frac{2}{3} \leqslant m \leqslant 1\right)$$

and when $\dfrac{\sigma X}{\alpha w}$ is large,

$$x_c \sim \lambda \alpha w^{\frac{1}{3}}.$$

At the age of 9–10, growth, which was beginning to slacken, accelerates. If the principal part of the growth is still to be represented by equation (2), k must be given a value at least equal to unity. Further, the form of the curves w and w' clearly shows the action of the limitative factors. In fact, the equation

$$w' = \varepsilon w - hw^2 - cwW,$$

with the parameters

$t_0 = 9$ yrs., $\varepsilon = \cdot 09$, $h = \cdot 000023$, $c = \cdot 000007$, expresses the observations very well.

How can the value $k = 1$ be physiologically interpreted? Return to equation, putting $k = 1$, and we get

$$f(w) = \frac{\varepsilon}{\gamma \alpha . th\left(\dfrac{\sigma X}{\alpha w}\right)};$$

in the two extreme cases, we have

$$f(w) = \frac{\varepsilon w}{\gamma \sigma X} \qquad \left(\frac{\sigma X}{\alpha w} \text{ small}\right)$$

$$f(w) = \frac{\varepsilon}{\gamma \alpha} \qquad \left(\frac{\sigma X}{\alpha w} \text{ large}\right).$$

It appears therefore that after 9–10 years the constructive energy is proportional to the net energy

obtained by the organism from its food. Hence at this age there is an abrupt passage from one stage to the next. This increased growth accompanied by a more complete constructive utilization necessarily provokes resistances which were absent in the earlier stage.

It might perhaps be possible to attribute this change to the beginning of the activity of the sex glands or perhaps to the combined action of these glands and others. On the whole it is at the age of 9–10 that the change takes place, and at 15–16 that growth reaches its maximum intensity. Without this hypothetical factor the organism would quickly die. Can there be seen in this factor, and in analogous factors appearing at critical moments, traces of the evolution of the species? It is quite possible that each species has passed through critical points and that the introduction of a new factor, developed and strengthened by selection, has enabled the species to survive.

A few words may be written on the linear growth of the body. The fifth column of the Table shows that the increase of stature, l', is very different from the function w'. The function l' decreases rapidly from $t = 0$ to $t = 4$ years, and also after 15 years; in the interval from 4 to 15 it remains almost constant. The last column of the Table gives the quotient $\dfrac{w^{\frac{1}{3}}}{l}$. If the growth of the body were homothetic, the ratio $\dfrac{w^{\frac{1}{3}}}{l}$ would remain constant. But this ratio first decreases, passes through a minimum about the 12th year, and then increases, which means that until the 12th year the increase in stature is more rapid and after the 12th year less rapid than that of weight.

This confirms the suggestion that a profound difference exists between increase in weight and increase in height, and explains the differences observed between the basal metabolism and the area of the body calculated from the formula

$$\text{Surface} \simeq \mu w^{\frac{2}{3}}.$$

2. MAMMALS

Problems of growth are not the same for warm-blooded and for cold-blooded animals. In the former,
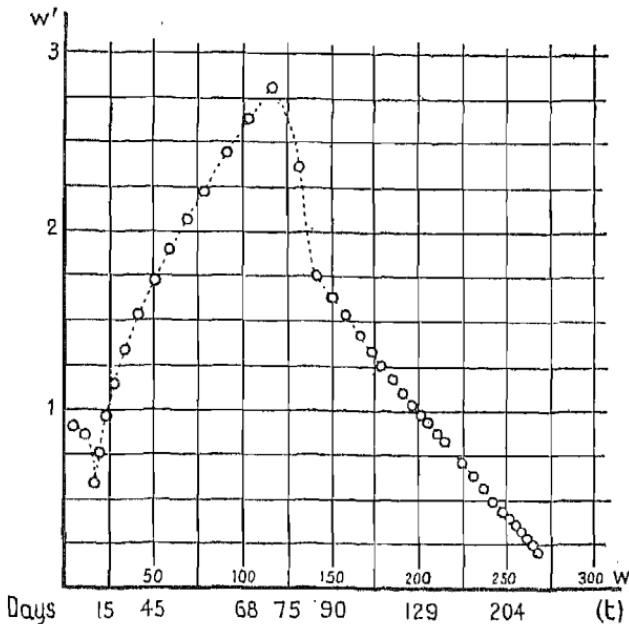

FIG. 13.—FUNCTION $w' = F(w)$ FOR THE RAT
after Donaldson.

as in man, there may be observed critical moments in the development, angular points in the growth-curve;

and the hope of expressing the growth of an animal by a simple formula has to be abandoned. This discontinuity of the growth-curve was first established by Lotka, and we owe the detailed study of the phenomenon to J. S. Huxley and G. Teissier.

Rats. Lotka, who treated the problem of growth as a statistician, noted that the first three months of a rat's life could be expressed by a logistic curve, but that later this curve gave values much lower than those observed in practice. As a matter of fact the first three months of the life of a rat are not very closely represented by the logistic curve. To confirm this, look at the empirical curve (1) for the rat (Fig. 13). Just as in man, it shows critical points. The first of these occurs at the age of twenty days and separates a phase of growth in which w' is almost constant from the following phase in which w' rapidly increases. This lasts until the 75th day, after which w' decreases fairly rapidly, almost in a straight line, and reaches zero on about the 290th day. Curve (1) shows clearly that the development of the rat consists of at least three different phases. It is curious that the differential equation

$$w' = \varepsilon w^{\frac{1}{4}} - h w^{\frac{3}{2}} \tag{12}$$

leads to a growth law of the type

$$w = A[th\lambda(t + \tau)]^{\frac{3}{2}} \tag{13}$$

which well represents the weight, w, of the rat during the whole of its growth, but curve (12) does not correspond at all to that in Fig. 13.

Guinea Pig, according to Minot. The growth curve of the guinea pig presented by Minot is a very interesting one. The curve (Fig. 14) passes through two maxima separated by a minimum. The first maximum

occurs on about the 15th day, the minimum about the 100th day, and the second maximum about the 180th. It looks as if the growth energy, weakened after the first maximum, experienced about the 100th day

|						
	100	200	300	400	500	600	700
Males	9	28	52	79	113	179
Females	8	28	52	88	140	204
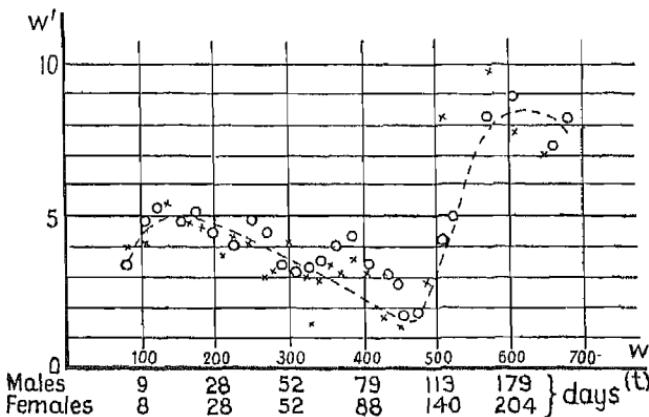
FIG. 14.—FUNCTION $w' = F(w)$ FOR THE GUINEA PIG
after Minot.

a recrudescence under the influence of a factor which had remained hidden until this moment. The phenomenon might be compared to a rejuvenescence of the organism.

The growth of the sheep is remarkably well represented by the equations

$$w' = a - bw, \qquad w = w - (w - w_0)e^{-at}, \qquad (14)$$

and this is true for several breeds.

In large cattle there is a critical point with the transfer from a milk diet to pasture. Similarly there are seasonal critical points corresponding to changes from summer to winter régime and vice versa. It seems that these changes not only affect the co-efficients,

but the exponents as well. Hence these seasonal variations must always be taken into account in the study of yearly statistics.

3. FISH

The growth of fishes also presents some interesting peculiarities. We have chosen an example which shows
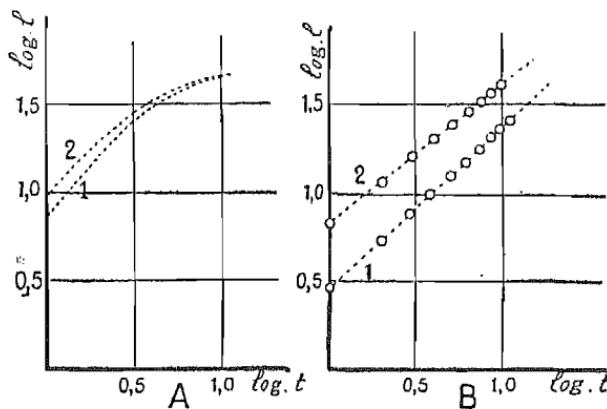

FIG. 15.—GROWTH OF THE BREAM, after Wasnetzoff
A. Southern Bream: 1. Volga—Caspian. 2. Azov.
B. Northern Bream: 1. L. Tuusula. 2. L. Pskov.

the importance of the geographical factor in splitting a species into varieties. Wasnetzoff gives very complete statistics of the growth of the bream in the fresh waters of the European parts of the Soviet Union. This vast region contains the basins of rivers flowing into four seas, and may be roughly subdivided into two parts, one of which feeds the Baltic and the Arctic Ocean, the other the Black Sea and the Caspian Sea. It seems that the growth of the bream in the northern half is governed by different laws from those in the south.

Fig. 15, A and B, gives a comparison between the growth-curves of the bream in these two regions. The abscissae represent the logarithm of the age and the ordinates the logarithm of the length of the body. It is seen that: (1) the original length of the northern bream is less than that of the southern; (2) the growth curve of the northern bream is almost rectilinear, while that of the southern curves towards the abscissa. The difference in original length may be explained by the action of climatic factors. The delayed action of the limitative factors in southern bream is more difficult to explain. Many hypotheses may be suggested of which the most plausible is that we are witnessing the appearance, perhaps already completed, of two varieties under the influence of different climatic factors.

The growth of the bream, in its initial stage, may be expressed by the formula

$$l = l_1 t^i.$$

The average values of l_1 and i for the two varieties are:

BREAM		l_1	i
Northern	.	5·1	·87
Southern	.	8·1	1·06

The values of i do not differ much from unity. The whole curve for the southern variety can be calculated from the formula

$$l = L - (L - l_0)c^{\frac{ht}{3}} \qquad (15)$$

which corresponds to the differential equations

$$l' = \frac{h}{3}(L - l), \qquad w' = \varepsilon w^{\frac{2}{3}} - hw \qquad (16)$$

o

The considerable deviation of the index i about the
average $i = 1$ may be explained by the fact that the
length is not proportional to the cube root of the weight.

4. GROWTH AND ECDYSIS

In many animals the relation between moulting and
growing takes an interesting mathematical form. In
arthropods linear growth between the moults is pre-
vented by the rigid chitinous skeleton, while increase
in weight continues to occur. At ecdysis the animal
rids itself of its tight skin, another more suited to its
weight replaces it, and the animal soon adapts itself
to the new régime. Przibram and Mégusar supposed
that the weight of an arthropod should be doubled
between one moult and the next, which corresponds
to a doubling of every cell in the body. In consequence
linear dimensions should increase from one moult to
the next in the proportion of $\sqrt[3]{2} = 1 \cdot 26$.

In spite of the existence of many aberrant cases this
rule has been confirmed by observation. In some
aberrant cases the linear dimensions are multiplied
after a moult by $1 \cdot 59 = 1 \cdot 26^2$ or by $2 = 1 \cdot 26^3$. Thus
Przibram's rule corresponds to an objective reality,
but there are many factors which may make growth
diverge from it. On the one hand, growth does not
always take place in a homothetic way: on the other,
the body of an animal has a complex internal and
external structure, and the organs and parts of the
body do not grow proportionately to its weight.

Finally, indefinite growth is impossible, for limiting
factors intervene in the invertebrates just as in the
vertebrates. These factors may act in two ways, either

by increasing the interval of time between two moults or by reducing the growth between one moult and the next. Lengthening of the time-interval is seen in several growth-curves, for example in *Dixippus morosus* and *Tenebrio molitor*. The curve for increase of weight between two moults in *Tenebrio molitor* resembles the growth-curves in the case of residual actions. The weight at first increases rapidly, then the increase is retarded, the weight reaches a maximum


Fig. 16.—Individual Growth of Tenebrio molitor, after Teissier. A, weight in function of time. B, spread of the antennae in function of time. *m*, *m*, minima corresponding to the moulds. M maximum shortly preceding a moult.

some time before the next moult, and finally decreases, but the moult intervenes and the next cycle begins.

It would be very interesting to determine the nature of the factor that produces this decrease of weight before a moult. Dehydration of the tissues may be suggested, as well as chemical action. It is a factor which may produce actions of the "hereditary" type, in the mathematical sense of the word, as the experiments of Ilyin have shown.

5. Growth of Organs and Parts of the Body

Denote by q the weight of an organ in an animal of total weight w. There is an empirical law connecting these two quantities

$$q = K w^t \qquad (17)$$

or, in logarithmic form

$$\log q = \log \text{K} + t \log w. \qquad (18)$$

This law is based upon a great number of observations, and within fairly wide limits of variation of w and q the growth-curve of q in relation to w is expressed in logarithmic co-ordinates by a straight line or by a broken line composed of straight elements. A question may be put here. What is the meaning of equation (17) and what are the values of i? If the growth of the organs were proportional to the weight of the body, then i would be equal to unity.

But i is almost always different from 1, and truth to tell there is no reason why it should equal 1. In many cases organs may be considered to be superficial formations. It is then not a matter of the outer surface of the body but the surface of the embryonic tissues, the foldings, invaginations and proliferations of which produce the development and structure of the body. It may be supposed that a superficial excrescence is nourished through the portion of the surface that it occupies, and if this portion is not too large the weight of the excrescence will be proportionate to this area and not to the weight of the body. I do not mean that things always occur in this way, but the hypothesis that i is different from 1 is in every case much more probable than that i should be equal to 1. G. Teissier calls laws of type (17) when the exponent i is different from 1, *laws of disharmony*. It would appear rather that there is not harmony when $i = 1$, and that there is not disharmony when i is different from 1.

To confirm this point of view, two numerical examples may be considered. In the particular case of the

rat's heart, $i = \cdot75$, a comparison with another em-
pirical law affords an explanation of this value of i.
The length of the rat's body also follows a law of
type (17)

$$l = Lw^{\cdot3} \qquad (19)$$

and the surface area of its body, s, can be represented
in the form

$$s = Sw^{\cdot7} \qquad (20)$$

Hence the weight of the rat's heart is proportional
to the area of its body.

The other case concerns the orthopteron *Dixippus
morosus*, of which G. Teissier has measured the total
length, the length of the abdomen, the length of the
prothorax, the length of the head and the diameter of
the eye at different periods of its life. Let w and l be
the weight and length of the body, w_1 and l_1 the weight
and length of the head, and w_2 and l_2 the weight and
diameter of the eye. Suppose that

$$l = Lw^{\frac{1}{3}}, \qquad l_1 = L_1w_1^{\frac{1}{3}}, \qquad l_2 = L_2w_2^{\frac{1}{3}}.$$

Suppose, now, that the head is a superficial excres-
cence of the body and the eye is a superficial excrescence
of the head. In such circumstances we get

$$w_1 = W_1w^{\frac{2}{3}} = Q_1l^2, \qquad w_2 = W_2w_1^{\frac{2}{3}} = Q_2l^3$$

and in consequence

$$l_1 = \lambda_1 l^{\frac{2}{3}}, \qquad l_2 = \lambda_2 l^{\frac{3}{3}}. \qquad (21)$$

Suppose that the length of the body increases pro-
portionately to a

$$l' = al.$$

Equations (21) show that the corresponding values of l_1 and l_2 become

$$l'_1 = \lambda_1 a^{\frac{2}{3}} l^{\frac{2}{3}}, \qquad l'_2 = \lambda_2 a^{3} l^{\frac{1}{3}}$$

and hence

$$\frac{l'}{l} = a, \qquad \frac{l'_1}{l_1} = a^{\frac{2}{3}}, \qquad \frac{l'_2}{l_2} = a^{\frac{1}{3}} \tag{22}$$

The following table gives the values observed by Teissier and those calculated from formulae (22):

l	15	19	28	37	46	64	85
l_1	1·15	1·35	1·65	2·1	2·6	3·1	3·8
l_2	·38	·43	·47	·57	·65	·75	·85
$a = \dfrac{l'}{l}$	1	1·27	1·87	2·47	3·07	4·27	5·67
$a^{\frac{2}{3}} = \dfrac{l'_1}{l_1}$ obs.	1	1·09	1·43	1·83	2·26	2·70	3·30
$\dfrac{l'_1}{l_1}$ calc.	1	1·17	1·52	1·83	2·12	2·62	3·18
$a^{\frac{1}{3}} = \dfrac{l'_2}{l_2}$ obs.	1	1·13	1·24	1·50	1·71	1·97	2·24
$\dfrac{l'_2}{l_2}$ calc.	1	1·11	1·32	1·49	1·64	1·90	2·16

If the uncertainty to which these measurements are subject be taken into account, it cannot be denied that the agreement is remarkable. The hypotheses used are very approximate and need many important corrections, but in this particular case they completely explain the observed phenomena.

CHAPTER XIV

FORMS OF LIVING OBJECTS

In this chapter we confine ourselves to a few remarks on the role of symmetry and polarity in the economy of an organism, and on the role of movement in the exterior shape of living objects.

1. Symmetry; Polarity

In most cases the forms of living objects are symmetrical either about a point, an axis, or a plane. Further, there are often poles or points of activity, either internal or peripheral, in situations that are related to the type of symmetry of the organism. This phenomenon may be explained by the *principle of economy of the organism,* a maximum result at a minimum cost, and by considerations of stability. From the mathematical point of view these two principles are united in the extreme problems, in which are sought the conditions causing an expression to assume an extreme value, either maximum or minimum. It is not possible to assert that all the forms of living animals are very satisfactory in this respect, but a general tendency is undeniable.

Sphere. Begin with the spherical form. Of all bodies of the same surface area the sphere has the largest volume, and of all bodies of the same volume the sphere has the smallest surface. These two extreme principles are of importance in the exchanges between

a living object and its environment. When these geometrical considerations are supplemented by a study of physical and chemical forces, the sphere becomes the figure of equilibrium. Thus a convex mass of liquid, either homogeneous or heterogeneous and stratified, assumes the form of a sphere under the action of hydrostatic pressure, osmotic pressure, capillary attraction, and viscosity, and it is the only form of equilibrium possible in the absence of other forces or of internal movement. If an irregular mass is divided into several parts it is very probable that these will take on a spheroidal form. If in a spheroidal mass the osmotic equilibrium with the surroundings is disturbed, the mass changes its volume but retains its spheroidal form.

Spheroidal and Ellipsoidal Forms. Radial symmetry can be preserved when the living mass contains a focus of activity nearly coincident with its geometrical centre, but this is relatively uncommon ; hence the appearance of a focus of activity produces a change from the spheroidal to the elongated or flattened ellipsoidal forms. The intervention of the force of gravity produces a non-concentric distribution of the materials composing a cell. An internal complexity due to one of these causes or to their combined actions changes a spheroidal body by creating an axial in place of a radial symmetry. A specialization of the surface accompanies this, with permeability, capillary tension and osmotic pressure varying from one pole to the other.

Movement. Suppose that an organism thus constituted comes to propel itself by ciliary action, pulsations, or any other method. In the case of vertical motion, axial symmetry may be retained; in horizontal motion

a deformation is produced, which increases as the normal speed of horizontal motion increases; and the body loses its axial symmetry, replacing it by symmetry about a plane. This is the commonest case.

Divisions. Consider now the disturbances of equilibrium utilized by organisms. The approach of other bodies may produce, directly or by induction, local changes of superficial permeability and the appearance of pseudopodia. In the same way the disappearance of the pseudopodia when the superficial stimulus ceases to act may be explained. It is curious that this phenomenon which appears to be so disadvantageous to the organism, should come at length to be used so profitably.

Cell-division is another form of equilibrium disturbance. In another connection Henri Poincaré, discussing the formation of the heavenly bodies, studied the problem of equilibrium-forms of a homogeneous fluid mass rotating under the Newtonian attraction of its particles. This problem, although very different from the one we are at present considering, nevertheless offers very useful analogies and suggestions. It is known that the spheroidal form of a heavenly body is stable; further it is known that the Earth–Moon system, composed of two spheroidal bodies, is stable. It must, however, be admitted that this system was formed by the break-up of a single gaseous mass, owing to the loss of stability. Consequently in comparing the present state of the Earth–Moon system with its hypothetical distant past, a single gaseous mass, we find a series of stable forms at the beginning and at the end, but losing their stability at some unknown intermediate moment. Similarly, a cell or a protozoon is relatively stable before division and the

two daughter cells become stable some time after division, but these two ends of a chain are separated by a link in which stability is disturbed. Henri Poincaré, discussing the series of equilibrium forms, has demonstrated the existence of critical points at which the series ceases to be stable, and stability then characterizes a new series of equilibrium forms. In this way the division of the gaseous mass into two separate masses is foreseen.

A similar phenomenon probably occurs with cells. The spheroidal form may be stable, while the forces in equilibrium satisfy certain inequalities, for example as long as the mass of the cell does not exceed a certain limit, depending on all the factors present. Near this limit stability vanishes and the smallest external action or the least internal asymmetry may produce a change of form or the division of the mass into two or more portions.

Division of a Fertile Egg. In the particular case of an egg there are four interesting circumstances: (1) an unfertilized egg possesses a really remarkable stability; (2) the first breakdown of stability is due to a foreign body penetrating as far as the nucleus, and the plane of the first division passes through the two poles of the egg and the path of the spermatozoon; (3) the divisions that follow have no need of external stimulus; (4) the first two divisions still keep a certain symmetry and produce four blastomeres to some extent similar to the original egg, while later divisions produce a deeper and deeper differentiation.

This last peculiarity is explained by the plane of the first division passing through the axis of symmetry. The four blastomeres resulting from the second division

have an elongated shape and are least stable in the equatorial region, which explains the orientation of the third division. Further the ahomothetic stratification of an egg explains the difference between the four micromeres and the four macromeres resulting from the third division. We shall not proceed to the later stages of the formation of a multicellular organism, although fairly simple geometrical and physical considerations seem able to explain some phases of the process.

What is less clear is the automatic mechanism which performs all these divisions after the first loss of stability. These uninterrupted divisions cannot be attributed to the presence of a foreign body, for parthenogenetic development obeys the same laws. Everything proceeds as if an essentially unstable system were held, pending the action of a releasing agent. This is very different from the division of unicellular organisms, producing in general a series of identical generations, separated by periods of stability.

2. ENVIRONMENT, MOVEMENT, AND FORM

The shape of a living organism depends in general on many and varied factors, but in certain cases the action of a small group of these factors dominates and wholly explains the external form. This is true of fishes, which lead an active mobile life in water, and sometimes out of it. By the phenomenon of convergence similar forms are found in other animals, very different from fish in origin and internal structure, but living in the same environment.

Consider first several experimental and theoretical

results from aero- and hydrodynamics. A body moving through a fluid needs a motor, a propeller, a method of changing speed and direction, and a stabilizer. The technical problem may have several more or less economical solutions.

First, horizontal motion must be distinguished from vertical motion. In horizontal movement in a liquid medium, without being supported on the bottom, there is a necessity for a propeller driven by a motor to produce, maintain, and modify the speed, and of a suspensor to preserve a certain level. Consider propulsion first. A propeller is opposed by the resistance of the medium and by friction. Resistance is proportional to the square of the velocity and to the density of the medium,

$$R = k\rho v^2$$

where R is the resistance, ρ the density, v the velocity, and k is a constant depending on the dimensions and shape of the body. Aerodynamic experiments show the sometimes enormous advantage of fish-shaped bodies over spheres, cylinders, and other forms. A fish-shaped body can move in a fluid with less effort than a much smaller sphere. The reason may perhaps be attributed to the formation in the surrounding fluid of discontinuities, separating regions of different conditions. Friction between the body and the medium is often negligible, but viscosity between two fluid regions of different conditions contributes to the formation of rotary movement, of whirlpools behind, before, and sometimes at the sides of the moving body, and these whirlpools increase the resistance to a remarkable extent. Sometimes they accompany the solid body as it moves when it is as if the propeller

were forced to drive the body itself plus the disturbed regions behind and before it; sometimes they detach themselves and their sucking action produces an increased resistance. But the whole system formed by these regions and the body itself presents a kind of fish-shaped figure. Suppose this system were solidified. The current admirably adapts itself to this fish-shaped model and the discontinuities due to the movements of such a body are overcome without the formation of dead water, whirlpools, etc. Experiment shows that for a given velocity there is an optimum relation between the dimensions of a fish-shaped body. If the body is too long, whirlpools appear at certain critical places on the lateral surface, if it is too short, whirlpools are formed in front and behind. Frédéric Houssay, to whom belongs the merit of having perceived this relation between the form and the movement of fish, also foresaw the existence of these critical spots, which coincide with the fins; he is mistaken only in the nature and exact role of the whirlpools, and hence his hydrodynamic analogies appear to be doubtful.

We pass on to vertical movement. The first thing to be done is reduce the difference between the weight of the body and the weight of liquid occupying the same volume. This little technical problem is very easy to solve in the case of water and the density of fishes differs very slightly from that of water. With air it is more difficult, and the specific gravity of birds and insects, though much reduced by a special arrangement of the tissues, still remains much higher than that of air.

Aeronautical technique admits four methods of vertical locomotion:

1. A special vertical propeller, as in helicopters.

2. Difference of specific gravity, as in balloons.

3. A horizontal propeller in conjunction with inclined planes.

4. Vertical currents in the atmosphere.

All these methods are used by living objects, and there are others which our technique has not succeeded in reproducing. The swim-bladder serves to change the specific gravity of fish, and is not intended for stabilization. The fins also seem to play the part of inclined planes. In some cases the whole body of the fish is transformed into an inclined wing, as in certain Trygonids, and these fish closely resemble aeroplanes or hydroplanes. This adaptation of form to medium makes all other modes of vertical displacement unnecessary, and very well illustrates the principle of economy.

There exists a fish able to propel itself in two media as different as air and water—the flying fish, whose extremely aerodynamic shape, with its well-developed pectoral fins, is altogether comparable to that of an aeroplane. In water the caudal fin acts as a propeller, with intermittent action, like the scull at the stern of a boat. This propeller gives the initial soaring movement which allows the fish to leave the water and accomplish a fairly long volplane. According to the experiments of Schouleïkine with a model of this fish placed in an air current in a wind tunnel, the support given by these fin-wings is quite enough to hold the fish up during its flight. It appears furthermore that the flying fish can make use of ascending air-currents.

We shall not linger over the form of birds, as this is a slightly more complicated example of the same

principle with a different propeller. It may merely be remarked that birds make great use of ascending air-currents, which enables them to reduce their expenditure of energy to a minimum.

CHAPTER XV

EVOLUTION

1. Life and Entropy

BEFORE attacking the problem of evolution, it is necessary to understand the exact meaning of the word. All existing definitions vary between two extremes. Some apply the word to any natural process whatever, contrasting evolution with immobility; others look for an expression of progress, describing as evolution all that is progressive, ascendant, and opposed to levelling. The former try to preserve an objective attitude, the latter paint the universe rose-coloured or black, according to their inclinations.

It seems to me that the word may be given a quantitative definition by applying it to every process that leads from a probable state to another less probable, or which is opposed to the increase of entropy. The objection to this definition may be that in applying it to partial processes or to ascending portions of cyclic processes, there is a risk of losing oneself in the intangible. But it is not necessary to do so. The distinction is very difficult to determine, as difficult as that in the paradox of the heap of corn. However, the heap exists and is very different from a grain. Evolution exists, and is very different from a particular, even an ascending, process.

Evolution local, Entropy universal. At this point a very important distinction must be established—between local tendencies and universal tendencies.

The latter will, without any doubt, move towards a more probable state, if this state is not already reached. Local tendencies may be ascendant or descendant and there is no doubt that the probability of the former is far less than that of the latter, but it is not zero. The realization of a slightly probable state is not impossible, and the non-realization of such a state is very slightly probable. Hence evolution must be a very rare phenomenon, highly localized both in time and space. Combinations that are very rare but which are more or less regularly realized may form a kind of separate universe, superimposed on chaos. If the appearance of matter is due to these chance combinations, each particle is a local phenomenon, but their aggregate may have a universal character and last a sufficiently long time to permit the realization of events much less probable but not impossible, such as living matter. Consequently life is a link in an ascending chain of very slightly probable events, the realization of which is in strict agreement with the calculus of probabilities. This ascent has not come to an end. Its latest stage is that which leads from the appearance of life to the appearance of human consciousness.

As a matter of fact this forward march is accompanied by a great wastage, and adaptation is inevitably accompanied by all the imperfections of Nature; all the species that have not succeeded, all the germs that have perished before maturation, before fertilization, before hatching. Each living object is in some way a winner in the lottery of life. Considered from this point of view the vital process ceases to be an exception to the law of entropy and becomes its most striking confirmation.

P

2. THE STRUGGLE FOR EXISTENCE. SELECTION

In the process of evolution, which has effected the transformation of species, what is the exact role of the struggle for existence? In the preceding chapters we have examined several cases in which a slight disadvantage has led to the total disappearance of one or other of the groups composing the population of a neighbourhood. We have seen that the disadvantage may be of a varied nature, but it always amounted to additions to the mortality. Hence the mechanism of elimination of the least adapted becomes quite clear when it concerns animals belonging to already existing species, but how can it apply to related groups belonging to the same species and giving fertile hybrids?

An example taken from Gause showed us a population composed of two different races of *Didinium nasutum* feeding on *Paramecium*. All was well in this little world as long as food was sufficient, but a scarcity of Paramecium led to a rapid disappearance of the giant strain of the predators, while the dwarf strain was able to survive for some time. What happens to the survivors of the dwarf strain on the reappearance of food? The population of Didinium is restored. By a mechanism which escapes us, but which is perhaps related to the behaviour of the chromosomes in conjugation, a giant mutation may reappear and multiply. It is to be supposed that their conjugations with the dwarf strain produce hybrids and that Mendel's laws determine the size of these hybrids and of their pure or mixed descendants.

In what follows we are not concerned with the mechanism of the appearance of mutations. We shall

consider a population which is composed in the first place of one hybrid and two pure groups. Each of these groups has its own vital co-efficients. In the case of one homogeneous isolated species the logistic equation

$$p^1 = np - mp - \nu p^2 - \mu p^2 \tag{1}$$

gives the increase in numbers of the species. The co-efficients of mortality m and μ do not require special treatment. Each group has its own. The co-efficients of fertility n and ν may vary in the different crossings according to which of the three groups includes the mating pair. In the simplest case there are nine types of crossing if the species is bisexual, and each type may have its particular fertility. Let p_1 and p_2 be the numbers of the two pure strains and p_3 that of the hybrids. If the crosses between individuals of these three groups are not controlled by any special law the number of births resulting from crossings between groups p_i and p_k must, without the intervention of limiting factors, be equal to $n_{ik}p_ip_k/p$ where

$$p = p_1 + p_2 + p_3. \tag{2}$$

Suppose that the action of these factors on the females decreases the fertility n_{ik} so that

$$\sigma_k = \nu_{1k}p_1 + \nu_{2k}p_2 + \nu_{3k}p_3$$

and the analogous action on the males has an effect

$$\tau_i = \rho_{i1}p_1 + \rho_{i2}p_2 + \rho_{i3}p_3.$$

In these circumstances the corrected co-efficient of fertility is

$$N_{ik} = n_{ik} - \sigma_k - \tau_i. \tag{3}$$

Further, the offspring of these crosses is distributed

according to Mendelian laws. We finally get the differential equations of the problem

$$
\left.\begin{aligned}
p'_1 &= \frac{N_{11}p_1{}^2}{p} + \frac{(N_{13}+N_{31})p_1 p_3}{2p} + \frac{N_{33}p_3{}^2}{4p} - m_1 p_1 \\
&\quad - p_1(\mu_{11}p_1 + \mu_{12}p_2 + \mu_{13}p_3) \\
p'_2 &= \frac{N_{22}p_2{}^2}{p} + \frac{(N_{23}+N_{32})p_2 p_3}{2p} + \frac{N_{33}p_3{}^2}{4p} \\
&\quad - m_2 p_2 - p_2(\mu_{21}p_1 + \mu_{22}p_2 + \mu_{23}p_3) \\
p'_3 &= \frac{(N_{12}+N_{21})p_1 p_2}{p} + \frac{(N_{13}+N_{31})p_1 p_3}{2p} \\
&\quad + \frac{(N_{23}+N_{32})p_2 p_3}{2p} + \frac{N_{33}p_3{}^2}{2p} \\
&\quad - m_3 p_3 - p_3(\mu_{31}p_1 + \mu_{32}p_2 + \mu_{33}p_3).
\end{aligned}\right\} \quad (4)
$$

The problem of selection appears in this form when it is concerned with two strains giving fertile hybrids. If other species inhabiting the same station are involved, system (4) must be completed by new terms and equations.

Consideration of equations (4) shows that:

1. In conditions unfavourable to the hybrids the more numerous pure strain will survive; consequently a new mutation which must necessarily be restricted in numbers has a very small chance of survival.

2. In conditions that are very favourable to the hybrids the three groups can co-exist and tend towards a stable equilibrium.

3. In the case in which the hybrids occupy an intermediate position between the two pure strains, only the pure group with the more favourable vital co-efficients survives.

We proceed to confirm these conclusions in a few relatively simple special cases.

Special Case 1. Suppose that the co-efficients v_{ik} and ρ_{ik} are zero and the only difference between the three groups consists of different mortalities. Equations (4) are simplified and become:

$$
\left.
\begin{aligned}
p'_1 &= \frac{n\left(p_1 + \dfrac{p_3}{2}\right)^2}{p} - m_1 p_1 - h p_1 p \\[2ex]
p'_2 &= \frac{n\left(p_2 + \dfrac{p_3}{2}\right)^2}{p} - m_2 p_2 - h p_2 p \\[2ex]
p'_3 &= \frac{2n\left(p_1 + \dfrac{p_3}{2}\right)\left(p_2 + \dfrac{p_3}{2}\right)}{p} - m_3 p_3 - h p_3 p
\end{aligned}
\right\} \quad (5)
$$

In the case of a low birth-rate less than the death-rate:

$$n < m_1, \qquad n < m_2; \qquad n < m_3 \qquad (6)$$

all three groups tend towards zero:

$$\lim_{t \to \infty} p_1 = \lim_{t \to \infty} p_2 = \lim_{t \to \infty} p_3 = 0 \qquad (7)$$

If the death-rate of the first pure strain is low

$$n > m_1, \qquad m_3 > m_1 \qquad (8)$$

the hybrids and the second pure strain vanish, and we get

$$\lim_{t \to \infty} p_1 = \frac{n - m_1}{h}, \ \lim_{t \to \infty} p_2 = 0, \ \lim_{t \to \infty} p_3 = 0. \qquad (9)$$

If the death-rate of the second pure strain is low

$$n > m_2, \qquad m_3 > m_2 \qquad (10)$$

the hybrids and the first pure strain disappear:

$$\lim_{t \to \infty} p_1 = 0, \ \lim_{t \to \infty} p_2 = \frac{n - m_2}{h}, \ \lim_{t \to \infty} p_3 = 0. \quad (11)$$

This implies that the survivor of the pure strains is the one whose co-efficient of increase is positive and whose death-rate is lower than that of the hybrids. What happens if the inequalities (8) and (10) are both realized? In this case, as has already been said, everything depends on the original values of $p_1(0)$, $p_2(0)$, and $p_3(0)$, and the less numerous of the pure strains vanishes with all the hybrids. Finally, in circumstances that are very favourable to the hybrids,

$$m_3 \ll m_1, \qquad m_3 \ll m_2 \qquad (12)$$

co-existence of the three groups is possible.

When the value of m_3 lies between m_1 and m_2, the survivor will be the pure strain whose death-rate is lowest and whose co-efficient of increase is positive.

Special Case 2. Take another case in which the co-efficients ν_{ik} and ρ_{ik} are zero, the death-rate and the limiting factors are the same for all groups, but fertility varies according to the crossing. To fix our ideas put

$$n_{11} = n_1, \ n_{22} = n_2, \ n_{ik} = \frac{n_{ii} + n_{kk}}{2}, \qquad (13)$$

that is to say, fertility in the hybrids is intermediate between those in the pure strains. In this way we get

$$\left. \begin{aligned} n_{33} &= n_{12} = n_{21} = \frac{n_1 + n_2}{2} \\[2mm] n_{13} &= n_{31} = \frac{3n_1 + n_2}{4} \\[2mm] n_{23} &= n_{32} = \frac{3n_2 + n_1}{4} \end{aligned} \right\} \qquad (14)$$

Equations (4) then become

$$
\left.
\begin{aligned}
p'_1 &= \frac{n_1 p_1{}^2}{p} + \frac{(3n_1 + n_2)p_1 p_3}{4p} + \frac{(n_1 + n_2)p_3{}^2}{8p} \\
&\quad - m p_1 - h p_1 p \\
p'_2 &= \frac{n_2 p_2{}^2}{p} + \frac{(3n_2 + n_1)p_2 p_3}{4p} + \frac{(n_1 + n_2)p_3{}^2}{8p} \\
&\quad - m p_2 - h p_2 p \\
p'_3 &= \frac{(3n_1 + n_2)p_1 p_3}{4p} + \frac{(3n_2 + n_1)p_2 p_3}{4p} \\
&\quad + \frac{(n_1 + n_2)p_1 p_2}{p} + \frac{(n_1 + n_2)p_3{}^2}{4p} \\
&\quad - m p_3 - h p_3 p.
\end{aligned}
\right\}
\tag{15}
$$

The three states of equilibrium are in this case inconsistent with one another. In the first case, in which fertility is low

$$
n_1 < m, \qquad n_2 < m \tag{16}
$$

all groups vanish.

In the second case the co-efficient of increase of the first pure strain is positive and its fertility is greater than that of the second pure strain:

$$
n_1 > m, \qquad n_1 > n_2 \tag{17}
$$

which in the limit leads to the survival of the first pure strain:

$$
\lim_{t \to \infty} p_1 = \frac{n_1 - m}{h}, \; \lim_{t \to \infty} p_2 = 0, \; \lim_{t \to \infty} p_3 = 0. \tag{18}
$$

The third case is the opposite of the second:

$$
\left.
\begin{aligned}
& n_2 > m, \qquad n_2 > n_1 \\
& \lim_{t \to \infty} p_1 = 0, \; \lim_{t \to \infty} p_2 = \frac{n_2 - m}{h}, \; \lim_{t \to \infty} p_3 = 0.
\end{aligned}
\right\}
\tag{19}
$$

Thus in this case the most fertile strain alone survives, provided its co-efficient of increase is positive.

Special Case 3. Suppose that the fertility and mortality are the same for all groups and all crossings, and that the limiting co-efficients satisfy the following relations:

$$\rho_{ik} = \nu_{ik} = 0, \ \mu_{1k} = \mu_1, \ \mu_{2k} = \mu_2, \ \mu_{3k} = \mu_3$$

so that equations (4) become

$$\left. \begin{aligned} p'_1 &= \frac{n\left(p_1 + \dfrac{p_3}{2}\right)^2}{p} - mp_1 - \mu_1 p_1 p \\ p'_2 &= \frac{n\left(p_2 + \dfrac{p_3}{2}\right)^2}{p} - mp_2 - \mu_2 p_2 p \\ p'_3 &= \frac{2n\left(p_1 + \dfrac{p_3}{2}\right)\left(p_2 + \dfrac{p_3}{2}\right)}{p} - mp_3 - \mu_3 p_3 p \end{aligned} \right\} \quad (20)$$

Everything depends on the limiting co-efficient μ_3 of the hybrid group. Suppose that $n - m > 0$ and that μ_3 is intermediate between μ_1 and μ_2. In this case the most resistant pure strain will survive, that which has the smallest limiting co-efficient.

Suppose again that

$$\mu_3 > \mu_2, \quad \mu_3 > \mu_1, \quad n - m > 0.$$

In this case the less numerous group disappears very quickly and so does the hybrid group.

Finally, in circumstances that are very favourable to the hybrids, with

$$\mu_3 \ll \mu_1, \quad \mu_3 \ll \mu_2, \quad n - m > 0$$

the three groups can co-exist.

Thus the final result of this discussion is in agreement with our conclusions.

3. INDIRECT SELECTION

Suppose that a species p composed of two pure strains p_1 and p_2 and their hybrids p_3 occupies a station in conditions favourable to the hybrids. Equilibrium is established and maintained until the appearance of another species x, which upsets the equilibrium in this little world. The mathematical and biological problem which results from this is too complex to be attacked here in general terms, and so we confine ourselves to the study of a particular case. Suppose, to fix our ideas, that the new species x serves as food for the species p; the equations of the system have the following form:

$$
\left.
\begin{aligned}
p'_1 &= \frac{n\left(p_1 + \dfrac{p_3}{2}\right)^2}{p} - mp_1 - hp_1p + l_1p_1x \\[2mm]
p'_2 &= \frac{n\left(p_2 + \dfrac{p_3}{2}\right)^2}{p} - mp_2 - hp_2p + l_2p_2x \\[2mm]
p'_3 &= \frac{2n\left(p_1 + \dfrac{p_3}{2}\right)\left(p_2 + \dfrac{p_3}{2}\right)}{p} - Mp_3 \\
&\qquad\qquad - hp_3p + l_3p_3x \\[2mm]
x' &= Ex - Hx^2 - \lambda x(l_1p_1 + l_2p_2 + l_3p_3)
\end{aligned}
\right\}
\tag{21}
$$

also $\qquad M \ll m$, and $\quad \varepsilon = n - m > 0$ $\qquad$ (22)

Suppose first that the fertility n is fairly large and

the co-efficients of utilization of the food satisfy the following inequalities:

$$l_1 \gg l_3, \qquad h\mathrm{E} > \varepsilon \lambda l_1$$

These conditions are favourable to the first pure strain, and result in the ultimate disappearance of the second and of the hybrids. The first pure strain survives in a state of equilibrium with the food-species

$$\left.\begin{aligned}
\lim p_1 &= \frac{\mathrm{E}l_1 + \varepsilon\mathrm{H}}{\lambda l_1{}^2 + \mathrm{H}h} \\
\lim p_2 &= 0, \qquad \lim p_3 = 0 \\
\lim x &= \frac{h\mathrm{E} - \varepsilon\lambda l_1}{\lambda l_1{}^2 + \mathrm{H}h}
\end{aligned}\right\} \qquad (23)$$

If the second pure strain is favoured

$$l_2 \gg l_3, \qquad h\mathrm{E} > \varepsilon \lambda l_2$$

when

$$\left.\begin{aligned}
\lim p_1 &= 0 \\
\lim p_2 &= \frac{\mathrm{E}l_2 + \varepsilon\mathrm{H}}{\lambda l_2{}^2 + \mathrm{H}h} \\
\lim p_3 &= 0 \\
\lim x &= \frac{h\mathrm{E} - \varepsilon\lambda l_2}{\lambda l_2{}^2 + \mathrm{H}h}
\end{aligned}\right\} \qquad (24)$$

In the case of insufficient multiplication,

$$\varepsilon < -\frac{l_k\mathrm{E}}{\mathrm{H}}, \qquad (k = 1, 2, 3) \qquad (25)$$

the predatory species vanishes:

$$\lim p_1 = \lim p_2 = \lim p_3 = 0, \quad \lim x = \frac{\mathrm{E}}{\mathrm{H}} \qquad (26)$$

Finally, if l_3 is large enough and ε is positive, the co-existence of the three predatory groups and their prey is not impossible. Thus the ultimate fate of the system depends chiefly on the hybrid group and especially on the l_3, the co-efficient of utilization of food. If l_3 is intermediate between l_1 and l_2, the survivor is the pure strain that makes greatest use of its food. If the hybrids make less efficient use of the food than either of the pure strains, the result depends on the initial composition of the predatory species. If the hybrids make better use of the food the co-existence of the three groups and their prey is possible. It goes without saying that supplementary conditions expressed in inequalities are in every case essential in order that these conclusions may be valid.

All these phenomena remain possibilities if ε is negative, that is to say when species x constitutes almost the sole diet of species p, with the proviso, however, that inequalities (25) are not satisfied.

No doubts can therefore be entertained as to the reality of the working of selection. In the case of two closely allied species which do not produce hybrids, the probability of the disappearance of the less favoured species is greater than that of the co-existence of the two. In the case of two strains which produce hybrids, the ultimate fate of these strains depends on the vital co-efficients of the hybrids. If the hybrids are less favoured than the pure strains, it is most probable that the less numerous strain will disappear, and this fact determines the fate of all mutations that produce feeble hybrids. In contrary circumstances the co-existence of the three groups is possible, and in the intermediate case the more favoured pure strain alone

will survive. This is what happens when all the characters of the hybrids are either dominated by those of one of the pure strains or are intermediate between those of the two pure strains.

The words "more favoured" and "less favoured" are very vague. We have tried to replace them by inequalities connecting the vital co-efficients and to make a separate study of the action of the three chief groups of factors, and the conclusions obtained are in complete agreement with actually observed results.

Two points remain obscure—the causes of the appearance of mutations and the number of varieties that a species may include. The two problems are not independent of each other. Everything would seem to depend on the initial and the final distribution of the genes in the chromosomes. Physical and chemical factors may act in this process, and it may be asked whether in critical circumstances a sudden change in external conditions may not produce abnormal distributions, some of which may be advantageous and permanent.

It seems further that the number of stable genetic arrangements is considerable and that the phenotype may show almost continuous variation. We cannot go into details of this mechanism in the chromosomes. What is important is the possibility of almost unlimited variation in a species by the working of two independent mechanisms—selection and the appearance of mutations.

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